Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

Volume 36, No. 1, January 1979

Volume 36, nº 1, janvier 1979

Fisheries and Oceans Canada

Pêches et Océans Canada

Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

Fisheries and Oceans Canada
Scientific Information and Publications Branch
Ottawa K1A 0E6

Pêches et Océans Canada
Direction de l'information et des publications scientifiques
Ottawa K1A 0E6

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Journal of the Fisheries Research Board of Canada

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Phytoplankton Ecology of Vancouver Harbor

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STOCKNER, J. G., AND D. D. CLIFF. 1979. Phytoplankton ecology of Vancouver Harbor. J. Fish. Res. Board Can. 36: 1–10.

Phytoplankton production and distribution were examined over a 2-yr period in the Burrard Inlet system, which includes a true fiord (Indian Arm), a shallow blind inlet (Port Moody Arm), and a turbulent narrows region that is contiguous to the Port of Vancouver. Greatest annual production occurred in Port Moody Arm with a mean of 532 g $C \cdot m^{-2} \cdot yr^{-1}$ while the lowest values were in Indian Arm and the Narrows region, averaging about 260 g $C \cdot m^{-2} \cdot yr^{-1}$. Nitrate and zooplankton grazing were the main factors limiting phytoplankton production in Indian Arm, while flushing and poor light conditions influenced phytoplankton growth in the Narrows and outer Burrard Inlet. Most of the discharges of domestic and industrial wastes have been diverted to the Fraser River, and Vancouver Harbor can be considered relatively clean and pollution-free because of strong tidal mixing and seaward flushing. The only sign of eutrophication in the inlet is in Port Moody Arm where sufficient nutrients from sewage discharges and a relatively stable mixed-layer depth create near optimal conditions for phytoplankton growth. Daily production here is among the highest recorded in the literature for Pacific coastal marine waters.

Key words: Phytoplankton, primary production, coastal marine embayment, fiord, phytoplankton succession and distribution, chlorophyll *a*

STOCKNER, J. G., AND D. D. CLIFF. 1979. Phytoplankton ecology of Vancouver Harbor. J. Fish. Res. Board Can. 36: 1–10.

Nous avons étudié sur une période de 2 ans la production et la distribution du phytoplancton dans le réseau de l'inlet Burrard, qui comprend un fjord véritable (le bras Indian), un bras de mer peu profond et en cul-de-sac (le bras Port Moody) et une région de goulet turbulent contiguë au port de Vancouver. La production annuelle maximale se trouve dans le bras Port Moody, avec une moyenne de 532 g $C \cdot m^{-2} \cdot a^{-1}$, alors que la valeur minimale est dans la région du bras Indian et du goulet, étant en moyenne d'environ 260 g $C \cdot m^{-2} \cdot a^{-1}$. Les principaux facteurs limitatifs de la production phytoplanctonique dans le bras Indian sont les nitrates et le broutage par le zooplancton, alors que dans le goulet et l'inlet Burrard le taux de vidange et de mauvaises conditions lumineuses affectent la croissance du phytoplancton. La plupart des effluents d'eaux usées domestiques et

Printed in Canada (J5118)
Imprimé au Canada (J5118)

industrielles ont été détournés vers le fleuve Fraser et l'on peut considérer le havre de Vancouver comme étant relativement propre et non pollué, à cause du fort brassage dû à la marée et de la vidange vers la mer. Le seul signe d'eutrophisation du réseau se trouve dans le bras Port Moody où suffisamment d'éléments nutritifs en provenance des égouts et une profondeur relativement stable de la couche mélangée créent des conditions quasi optimales de croissance phytoplanctonique. La production quotidienne à cet endroit est parmi les plus élevées enregistrées dans les travaux publiés sur les eaux marines côtières du Pacifique.

Received January 30, 1978
Accepted September 28, 1978

Reçu le 30 janvier 1978
Accepté le 28 septembre 1978

THE city of Vancouver is a rapidly growing population center bordering the shores of Burrard Inlet, which includes Indian and Port Moody arms. As industrial and commercial development grows, the discharge of industrial and domestic effluent to the sea increases, and it becomes essential for scientists to assess the impact of these effluents on the marine receiving waters.

Past physical–chemical studies included those of Carter (1934) and Gilmartin (1962) in Indian Arm, Waldichuk (1957, 1965) and Waldichuk et al. (1968a, 1968b) in Port Moody, Burrard Inlet, and the adjoining Georgia Strait, and Tabata (1971), who described the physical oceanography of the entire harbor area. Biological studies include those by Gilmartin (1964) and Buchanan (1966) in Indian Arm, Stockner et al. (1977) and Stockner and Cliff (1976) in the adjoining Howe Sound, and Parsons et al. (1969a, 1969b) and Takahashi et al. (1973) on the Fraser River plume.

The objectives of this work were (1) to present new descriptive information on the phytoplankton ecology of the Indian Arm–Burrard Inlet fiord system, (2) to assess effects of freshwater inflow, tidal mixing, and industrial and domestic effluents on plankton distribution and production, and (3) to relate primary production rates in Burrard Inlet to adjacent coastal waters, and to compare these with world literature values.

Description of the Study Area

The study area may be divided into three main sections: outer Burrard Inlet (outer Vancouver Harbor west of First Narrows), inner Burrard Inlet (Vancouver Harbor from First Narrows to mouth of Port Moody Arm), and Port Moody and Indian arms (Fig. 1). Rainfall is highly variable due to the influence of high mountains, and averages about 1.75 $m \cdot yr^{-1}$. Tides in the Burrard Inlet system are of the mixed type, with a large diurnal inequality between magnitude and timing of highs. The mean range is 3.1 m, with a maximum of 4.9 m. At both the First and Second narrows, maximum tidal currents can attain speeds in excess of 6 knots (11 $km \cdot h^{-1}$) during both flood and ebb stages.

Outer Burrard Inlet

The seaward boundary of the outer inlet extends into the Strait of Georgia on a line running from Point Grey to Point Atkinson (Fig. 1). The major freshwater source influencing this area is the Fraser River, with a minimum discharge of 1133 $m^3 \cdot s^{-1}$ and a maximum of >11 330 $m^3 \cdot s^{-1}$. During much of the phytoplankton growing season,

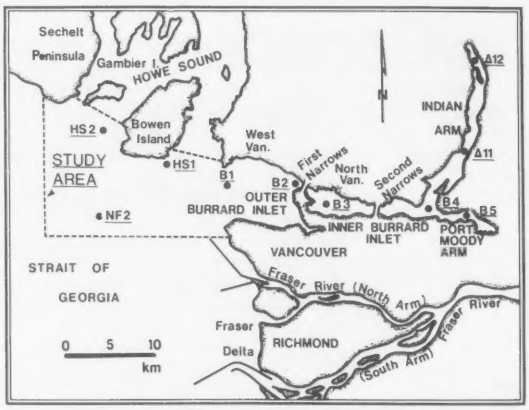

FIG. 1. Burrard Inlet system with station locations.

silty Fraser River discharge imparts an opaque color to the surface layer in this region. Other sources of freshwater include the Capilano River with a range in discharge from 4.5 to 25 $m^3 \cdot s^{-1}$, several small North Shore streams, and the Squamish River discharging to Howe Sound.

Inner Burrard Inlet

Because Burrard Inlet is relatively shallow, has no true sill, and lacks close precipitous mountain walls, it cannot be considered a typical fiord. It is 23.2 km long, and varies in width from 0.46 km (First and Second narrows) to a maximum of 3.7 km (center of harbor). The mean depth of the inlet is 21 m, with a maximum depth of 66 m. The major freshwater source to the inlet is the Seymour River, ranging in discharge from 2.8 to 23.3 $m^3 \cdot s^{-1}$. There are four other streams discharging to the inlet, but the flow of each is an order of magnitude less than that of the Seymour River. Inner Burrard Inlet is continually flushed by strong tidal currents, and net surface water flow is seaward.

Indian and Port Moody Arms

Indian Arm is a true fiord and has been described by Gilmartin (1962, 1964). It is 22.1 km long and has an average width of 1.3 km. The average depth is 200 m (maximum 245 m), and near its mouth the inlet shoals to a sill depth of 26 m. The major freshwater inputs are from (a) the Indian River, (b) the Buntzen power plant, and (c) the many small peripheral streams surrounding Indian

Arm. Estimated freshwater input ranges from a 9.91 $m^3 \cdot s^{-1}$ minimum to a 52.39 $m^3 \cdot s^{-1}$ maximum (Gilmartin 1962). Indian Arm is considered a positive estuary where precipitation and runoff exceed evaporation, resulting in a net seaward surface flow.

Port Moody Arm is a short inlet (6.5 km) with little local runoff and no inflow from large permanent streams. It is a shallow inlet with a mean depth of 9 m and maximum of 24 m. The inlet was classified as a *fiard* by Carter (1934) because of its shallowness, lack of sill, and absence of major inflows. In summer when freshwater inputs are near zero, evaporation often exceeds precipitation and runoff (Waldichuk 1965). Considerable industrial development occurs on its shores and some industrial and domestic wastes are discharged without treatment to the inlet.

Materials and Methods

Stations in the Burrard Inlet system were occupied monthly, commencing January 1975 and ending December 1976.

Total incident solar radiation was recorded on a Belfort pyrheliometer, located at Pacific Environment Institute on the north shore of outer Burrard Inlet. Extinction of surface light with depth was measured by a Montedoro–Whitney Underwater Illuminance meter (Model LMT-8A). The natural logarithm of light intensity was plotted against depth, and the slope of a straight line fitted to the points by linear regression provided an estimate of the mean downward extinction coefficient, k. A standard 30-cm white Secchi disk was used to measure water transparency at every primary production station.

Temperature profiles to a depth of 50 m were obtained with a bathythermograph (B.T.). A bucket thermometer was used to measure surface temperatures for B.T. calibration.

Water samples were collected from 1-, 3-, 5-, and 20-m depths and later analyzed for the following parameters: total carbonate carbon, salinity, dissolved oxygen, and nutrients (NO_3^{-1}, PO_4^{-3}, and SiO_4^{-4}). Total carbonate carbon was measured using an Orion digital pH meter (Model 801), and the method of Strickland and Parsons (1968) was used to determine carbonate alkalinity. However, if after acid titration final pH values fell below 3.00, then the sample analysis was repeated using the APHA (1971) standard titrimetric method. Salinity was analyzed with an Auto-lab salinometer (Model 601) to an accuracy of ±0.5‰. Density was computed by nomograph from temperature and salinity records. Dissolved oxygen (samples fixed within an hour of being taken) was determined by the Winkler titration method (Strickland and Parsons 1968). Samples for nutrient analysis were immediately frozen, and later analyzed by the Fisheries Operations/Environmental Protection Service analytical laboratories, Pacific Environment Institute, West Vancouver, using methods outlined in their manual (Fisheries/EPS 1974).

The standard ^{14}C method as initially proposed by Steemann–Nielsen (1952) was used, with some modifications. Water was collected from surface skim, 0.5-, 1-, 2-, 3-, 5-, 10-, and 20-m depths using a 6-L polyvinylchloride Van Dorn bottle. Productivity bottles (two 125 mL light and one 125 mL dark) were inoculated with 1 mL $NaH^{14}CO_3$ (3.7×10^{-5} GBq·mL^{-1}). For each experiment, the number of disintegrations per minute (dpm) per millilitre was determined by placing 1 mL of stock solution in each of three scintillation vials. In most cases, samples were incubated for 4–5 h, normally from 09:30 to 14:30. Water was filtered at a vacuum not exceeding 20 cm Hg through 0.45-μm BDH cellulose nitrate filters and placed in 10 mL of a toluene-based fluor (POPOP, PPO, 2-ethoxyethanol, and toluene). Samples were analyzed within 24 h for activity in a Packard Tri-Carb Liquid Scintillation Spectrometer (Model 3375) and data processed on a Hewlett-Packard Calculator Plotter (Model 9820A). The equation of Strickland (1960) was used to convert dpm's to milligrams carbon per cubic metre per hour. Using incident solar radiation for the entire light-day and for the incubation period, data were converted to milligrams carbon per cubic metre per day and integrated by a Hewlett-Packard Plotter (Model 9862A) to give phytoplankton production on an area basis (mg C·m^{-2}·d^{-1}). This involved linear interpolation between data points to the depths where light and dark uptake were equal. Phytoplankton samples from 1 and 5 m were preserved in acetate Lugol's solution and enumerated using the Utermöhl (1958) sedimentation method. Volumes were determined using values computed by Stockner and Cliff (1976). Each phytoplankton sample was examined under 175 and 700 × magnification using a Wild M40 inverted plankton microscope. Results were expressed as cells and total volume per cubic metre.

One litre of seawater was taken for chlorophyll *a* analysis from 1-, 3-, 5-, and 20-m depths, and filtered onto Whatman GF/C glass fiber filters with a small amount of $MgCO_3$ added. Within 1 wk frozen filters were macerated in a tissue grinder with 10 mL of 90% acetone, and the filtrate analyzed on a Cary recording spectrophotometer (Model 15). The SCOR-UNESCO equation given in Strickland and Parsons (1968) was used to calculate chlorophyll *a*.

Vertical zooplankton hauls from 50 m were made at each station with a SCOR-UNESCO plankton net, with mouth diameter of 57 cm and screen mesh size of 350 μm. Samples were preserved in 5% Formalin, returned to the laboratory, and split into two equal subsamples. One portion was dried overnight at 90°C, and results expressed as zooplankton biomass in milligrams (dry weight) per cubic metre. The other portion was preserved for future reference.

Results

Physicochemical Parameters

Burrard Inlet presented a varied set of oceanographic conditions brought about mainly by a wide range of basin morphometric features and by strong tidal currents. Monthly surface water temperatures paralleled air temperature, reaching maximum values (>20°C) in July and August. Temperatures at depths >20 m showed less variation and ranged from 6 to 12°C. By mid-April or early May a stable surface layer was formed by pronounced salinity–density gradients. The mixed layer depth varied from a very stable 3–5-m depth in Indian and Port Moody arms to 7–9 m in outer Burrard Inlet, where winds, tidal currents, and Fraser River discharge caused greater spatial and temporal variability (Table 1).

In summer, surface layer salinities ranged from 7 to 20‰ while values at more stable, deeper depths averaged 26‰ (Table 1, Fig. 2). Due to entrainment by

TABLE 1. Maximum–minimum values and annual means of selected physical, chemical, and biological variables in the surface layer (0–5 m) of the Burrard Inlet system in 1975 and 1976.

Station	Temp. (°C)	Salinity (‰)	Density (σ_t)	Mixed layer depth (m)	Dissolved O_2 (mg·L^{-1})	NO_3-N (mg·L^{-1})	PO_4-P (mg·L^{-1})	SiO_4 as Si (mg·L^{-1})	Extinction coefficient (k)	Chlorophyll a (mg·m^{-2}) (0–20 m)	Primary production (g C·m^{-2}·yr^{-1}) (0–20 m)	Zooplankton biomass (mg·m^{-3})
Outer Burrard Inlet												
HS1	6.0–18.5	10.2–29.6	6.4–23.2	8.7	5.0–10.0	<0.01–0.39	0.01–0.10	0.50–2.75	0.16–1.33	<1.0–460.4	352	0.8–157.3
	10.8	22.1	16.6		6.9	0.15	0.06	1.11	0.47	41.9		21.0
HS2	5.5–18.8	12.8–28.9	9.2–22.6	8.0	5.2–10.0	<0.01–0.37	0.01–0.09	0.41–2.50	0.15–0.94	<1.0–479.3	265	1.2–319.8
	10.8	22.5	17.3		7.1	0.13	0.04	0.98	0.39	41.3		25.2
NF2	5.6–18.7	9.1–28.1	6.0–21.9	8.6	6.4–7.9	0.01–0.31	0.01–0.14	0.50–2.25	0.13–0.64	2.0–270.2	363	1.7–316.6
	10.8	22.5	17.1		7.3	0.12	0.05	1.10	0.36	54.1		54.5
B1	6.0–19.2	16.2–26.9	10.8–21.2	6.2	5.4–7.4	0.04–0.30	0.03–0.25	0.50–2.85	0.24–1.05	2.6–139.2	415	2.4–26.2
	11.6	21.8	16.4		6.5	0.21	0.08	1.20	0.50	37.9		9.9
B2	5.6–17.2	14.0–27.3	10.0–21.3	5.4	5.5–7.9	0.02–0.32	0.04–0.20	0.50–2.95	0.19–2.03	2.9–117.5	370	1.7–44.5
	11.3	20.7	15.7		6.7	0.15	0.07	1.25	0.57	41.3		13.6
Inner Burrard Inlet												
B3	6.5–15.3	19.7–28.6	14.4–22.2	3.7	4.3–7.6	0.12–0.33	0.05–0.09	0.50–1.95	0.25–0.54	3.4–254.5	254	1.2–32.1
	10.2	24.4	18.7		6.0	0.19	0.07	1.24	0.40	39.7		12.0
B4	6.6–15.7	16.6–25.9	12.9–20.2	4.5	4.6–8.5	0.01–0.34	0.03–0.09	0.50–2.35	0.21–0.55	3.4–306.6	375	1.0–106.5
	10.4	22.3	17.1		6.3	0.14	0.06	1.01	0.36	55.5		27.1
Port Moody Arm												
B5	6.9–18.2	17.3–25.7	13.4–19.3	4.3	4.4–9.3	0.01–0.32	0.04–0.14	0.50–1.90	0.30–0.68	3.3–333.6	532	0.6–152.9
	11.8	22.5	16.9		6.4	0.12	0.07	0.93	0.47	78.8		32.8
Indian Arm												
11	5.6–16.2	12.6–25.8	10.1–19.7	4.5	5.0–12.2	0.01–0.31	0.02–0.08	0.20–3.45	0.15–1.75	0.7–254.0	285	1.1–92.5
	10.4	20.7	16.0		7.1	0.11	0.05	0.88	0.34	31.2		15.0
12	5.7–16.8	6.9–27.0	11.3–21.1	6.1	3.2–11.7	0.01–0.33	0.02–0.09	0.20–2.30	0.13–3.91	1.2–491.9	273	1.1–87.1
	9.4	21.1	16.6		6.9	0.12	0.05	0.83	0.43	34.6		17.4

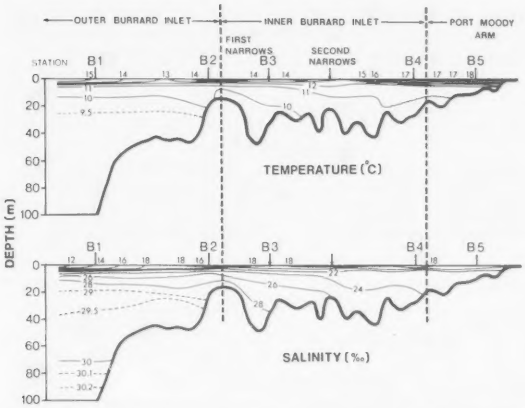

FIG. 2. Longitudinal section of Burrard Inlet with study station locations and temperature and salinity isoclines from July 7–9, 1966 (after Tabata 1971).

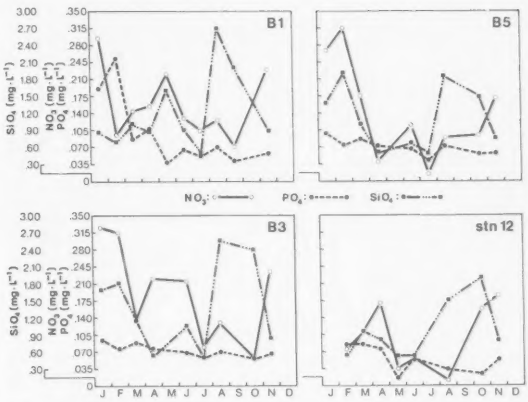

FIG. 3. Seasonal variation of surface values (0–5 m) in nitrate, phosphate, and silicate at selected stations in Burrard Inlet in 1976.

strong tidal currents at both narrows, surface salinities in inner Burrard Inlet were consistently higher than adjoining regions, averaging 18–20‰ during summer months. A halocline occurred throughout the year, shallow and weak in winter, becoming deeper and more stable by mid-April as spring runoff commenced. Variations in density (σ_t) followed patterns described for temperature and salinity, with highest values in January and lowest in May (Table 1).

Surface layer dissolved oxygen values showed similar seasonal trends in all study years, with peak values coincident with maximum phytoplankton biomass. Highest values were found in regions little influenced by strong tidal currents (Port Moody and Indian arms). The least seasonal variation in surface layer dissolved oxygen occurred in inner Burrard Inlet where turbulent mixing and entrainment created more vertically uniform oxygen concentrations.

Lowest values of carbonate carbon occurred during May and June when rivers were at peak discharge, and highest values occurred in winter months. Mean values at depths greater than 20 m ranged from 22 to 25 $\times 10^3$ mg C $\cdot$ m^{-3} while surface values exhibited much greater variation, ranging from 6 to 20 $\times 10^3$ mg C $\cdot$ m^{-3}.

Incident solar radiation showed typical temperate latitude variation with daily summer values ranging from 2428 to 2721 J $\cdot$ cm^{-2} and winter values of 42–251 J $\cdot$ cm^{-2}. Indian Arm received less radiation annually because of high mountains and greater cloud cover (Gilmartin 1962). Annual mean extinction coefficients (k) showed little variation in light attenuation among stations except at stations B1 and B2, where the influence of silty Fraser River water caused higher values (Table 1). Seasonally, Secchi depth showed trends similar to mean k.

Highest values of dissolved nitrate and silicate occurred in winter, as well as the most uniform depth distribution. At stations where stratification occurred (Indian and Port Moody arms), surface layer nitrate and silicate values fell to low levels commensurate with the vernal and/or autumnal phytoplankton blooms and remained low but variable throughout the summer, until restored to winter levels by deep mixing in October and November (Fig. 3). In regions with vertical instability caused by strong tidal mixing (B3 and outer Burrard Inlet stations), nitrate and silicate values in the surface layer were higher and more variable, with lows often occurring during the autumnal bloom in September (Fig. 3). Phosphate varied little seasonally and showed uniform concentrations at all stations. At 20 m, all nutrient values showed little seasonal variation. Inputs of nitrogen and phosphorus from several point sources within the study area undoubtedly contributed to the variability in seasonal nutrient concentrations in the Burrard Inlet system (Fig. 3). Highest mean concentrations of the three nutrients occurred in inner Burrard Inlet and the lowest in Indian Arm (Table 1).

BIOLOGICAL VARIABLES

The phytoplankton community of Burrard Inlet was composed of six major groups: diatoms, dinoflagellates, cryptophytes, silicoflagellates, small chrysophyceans, and euglenophytes. In total there were over 85 taxa, with diatoms and dinoflagellates (53 and 22 species, respectively) dominant. The most abundant species at all stations were *Skeletonema costatum*, *Chaetoceros* spp., and *Thalassiosira* spp. Seasonal variation of phytoplankton numbers and biomass in 1975 and 1976 was similar to that observed in the adjoining waters of Howe Sound (Stockner and Cliff 1976) and in Puget Sound (Winter et al. 1975) to the south.

The general trend at all stations was greater phytoplankton abundance at 1 than 5 m. The vernal bloom usually occurred in April or early May, sooner and

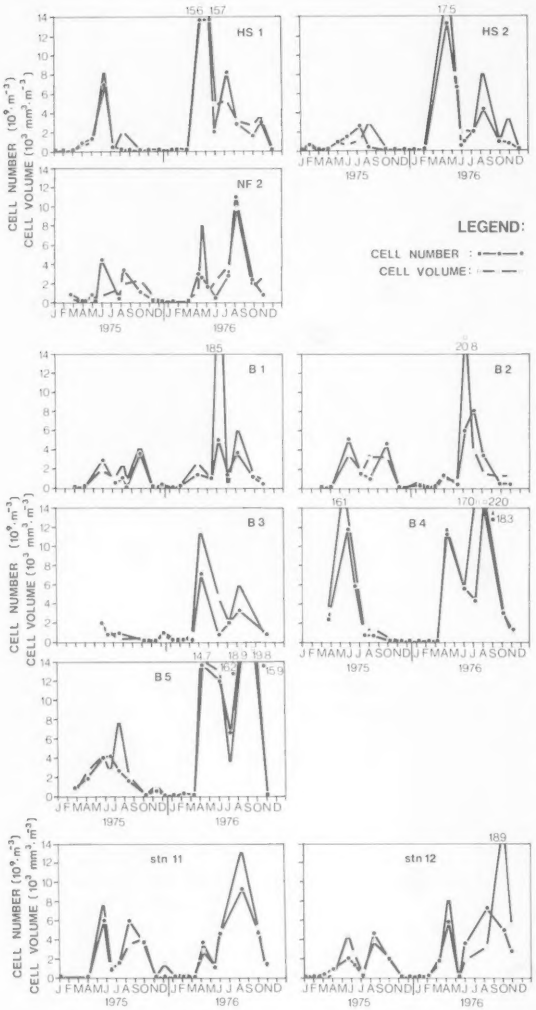

FIG. 4. Total phytoplankton volume and numbers at 1-m depth at stations in the Burrard Inlet system for 1975 and 1976.

more rapidly in the more stable stratified inner Burrard Inlet–Port Moody–Indian Arm area than in outer Burrard Inlet (Fig. 4). The autumnal peak was less distinct, smaller, and sustained over a greater period than the spring bloom in outer Burrard Inlet, but at most inner Burrard Inlet stations the fall peak was greater than the spring peak (Fig. 4). In July and early August, dinoflagellates were dominant, while spring and fall peaks were composed chiefly of diatoms (Table 2). Cloudy weather throughout the summer of 1975 led to the large disparity in annual production and

TABLE 2. Spring and fall phytoplankton bloom dominants (>5%) by volume in Burrard Inlet in 1975 and 1976 (percent of total phytoplankton volume is given in parentheses).

Spring	Fall
Outer Burrard Inlet	
Skeletonema costatum (33)	*Cerataulina bergonii* (33)
Cerataulina bergonii (31)	*Prorocentrum* sp. (7)
Thalassiosira spp. (22)	*Rhizosolenia* sp. (6)
Small chlorophyte (8)	Small chrysophyte (6)
Inner Burrard Inlet	
Skeletonema costatum (59)	*Skeletonema costatum* (55)
Coscinodiscus spp. (23)	*Thalassiothrix* sp. (13)
Thalassiosira spp. (8)	*Cerataulina bergonii* (10)
	Coscinodiscus spp. (6)
Indian and Port Moody Arms	
Skeletonema costatum (48)	*Skeletonema costatum* (37)
Thalassiosira spp. (36)	*Nitzschia* spp. (22)
Small chlorophyte (5)	*Exuviella* sp. (18)

phytoplankton biomass when compared with values from the more typical summer conditions observed in 1976 (Table 1 and Fig. 4).

Chlorophyll *a* values showed time and space variations similar to those discussed for phytoplankton (Fig. 5). Greatest amounts of chlorophyll occurred at Station B5 in the poorly flushed Port Moody Arm, with progressively lesser amounts seen at stations on a line moving seaward from Port Moody (B5) to Point Atkinson (B1) (Fig. 5). Moderate levels of chlorophyll existed at boundary stations in outer Burrard Inlet with the least occurring in Indian Arm.

The seaward trend of diminishing chlorophyll was not as obvious in plots of annual production (Fig. 5). Port Moody Arm was clearly the most productive region of Vancouver Harbor, followed by Point Atkinson (B1), mouth of Indian Arm (B4), and First Narrows (B2). The highest rate of 6.6 $g\,C \cdot m^{-2} \cdot d^{-1}$ occurred during the vernal bloom at Station 12 in Indian Arm, but it was not uncommon to observe daily values in excess of 4 $g\,C \cdot m^{-2}$ during spring or autumnal blooms at all stations. Following the vernal maximum in May and June, daily rates averaged 1–2 $g\,C \cdot m^{-2}$, and from November through to the following March, values were negligible (Fig. 5).

On a yearly basis Stations B1–B5 (except B3) were the most productive and B3 and Indian Arm stations the least (Table 1).

A single vertical zooplankton haul at each sampling led to large time and space variations among stations (Table 1 and Fig. 6). Peak zooplankton biomass lagged several weeks behind phytoplankton peaks. The greatest zooplankton biomass was found at Stations B5 in Port Moody Arm and B4 in water contiguous to it, where the greatest standing stock of phytoplankton occurred. In Indian Arm and to a lesser extent in the boundary waters of Howe Sound (HS1 and HS2), only a single

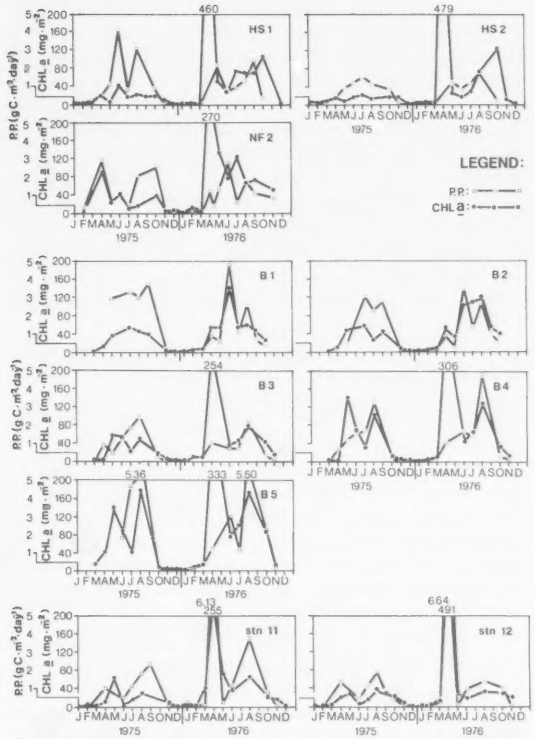

FIG. 5. Daily integral rates of primary production (PP) and integral chlorophyll *a* values (0–20 m) at stations in the Burrard Inlet system for 1975 and 1976.

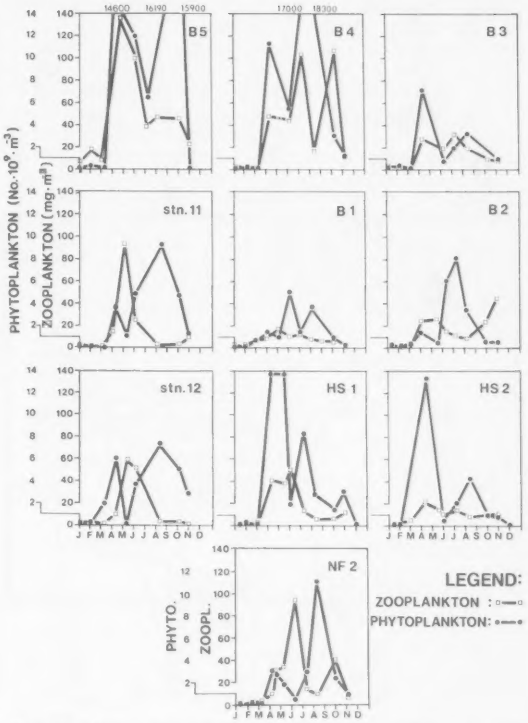

FIG. 6. Seasonal variation in zooplankton and phytoplankton standing stocks at stations in the Burrard Inlet system for 1976.

population peak occurred in May or June, while at most other stations in Burrard Inlet, a bimodal spring and fall population was evident.

Discussion

Carter (1934) and LeBrasseur (1954) observed that most south coast British Columbia fiords were "plankton poor" in their main body and "plankton rich" in boundary waters of the Strait of Georgia near their mouths. The Burrard Inlet system is atypical of most British Columbia fiords because of (1) the introduction of nutrients from both domestic and industrial waste effluents, (2) the discharge of clear water rivers (as opposed to glacially turbid river systems), (3) the strong tidal currents and associated turbulent mixing at both Narrows, and (4) the intrusion of turbid Fraser River water in summer. These features create a complex oceanographic system that markedly affects distribution and production of phytoplankton (Fig. 7).

Previous studies of phytoplankton in Indian Arm have documented the seasonal changes in abundance and distribution and shown that nitrate limitation and zooplankton grazing were the major factors limiting phytoplankton growth (Gilmartin 1964; Buchanan 1966). Our data from 1976 and 1977 supports these earlier findings by showing a significant correlation between phytoplankton biomass (chlorophyll *a*) and nitrate, zooplankton biomass, and light (stepwise multiple linear regression, $r = 0.93$). The vernal phytoplankton bloom in 1976 was rapidly depleted by an expanding zooplankton population (Fig. 6). In August, September, and October, large populations of jellyfish and hydroid medusae in the surface layer (*Aurelia aurita*, *Cyanea capillata*, and *Acquorea acquorea*) kept the zooplankton population low, enabling phytoplankton to attain far greater densities than seen in spring. In October–November, low nutrient and light levels, increased mixing, and seaward flushing contributed to the decline of the phytoplankton stocks in Indian Arm.

In Port Moody Arm, surface layer stability, sufficient nutrients, and low flushing rates created near optimal conditions for phytoplankton growth. As in algal batch cultures, exponential growth led quickly to a high population density in April which was sustained at relatively high levels throughout the growing season (Fig. 6). Phase lag correlation with zooplankton popu-

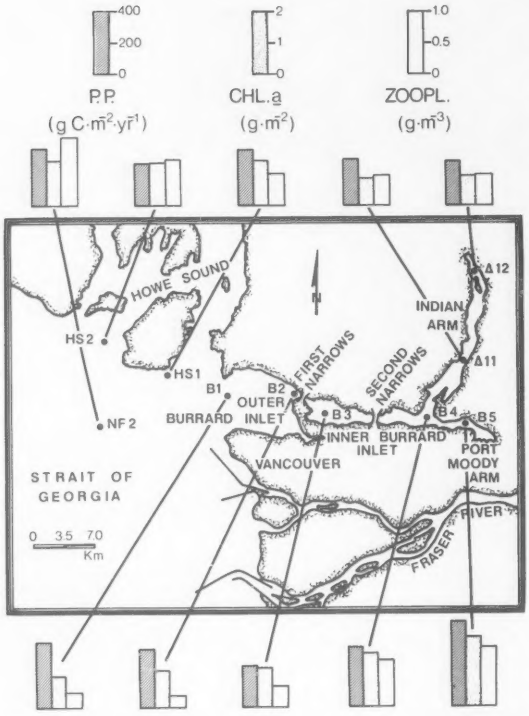

FIG. 7. Mean annual primary production, chlorophyll *a*, and zooplankton biomass at stations in the Burrard Inlet system for 1975 and 1976.

lations was not as apparent here as in Indian Arm (Fig. 6). Annual primary production rates, stocks of phytoplankton, and chlorophyll *a* levels were higher here than at any other station in Burrard Inlet (monthly paired *t*-test, $P = 0.05$) (Fig. 7).

Phytoplankton dynamics at Stations B2 and B3, within the inner harbor, were complicated by strong tidal mixing and the periodic intrusion of silty Fraser River water on large flood tides. Nutrient levels in the unstable surface layer were highest here during the growing season (monthly paired *t*-test, $P = 0.05$). The disparity in the distribution of phytoplankton biomass from Port Moody to outer Burrard Inlet was caused primarily by horizontal advection of viable cells in a net seaward direction (Tabata 1971).

Intrusion of silty Fraser River water throughout the summer was the primary factor affecting phytoplankton growth at Station B1 in the outer harbor (Fig. 6). Since the Howe Sound boundary stations and Station NF2 were not as strongly influenced by the Fraser River plume, grazing and nutrient depletion were of greater importance to phytoplankton dynamics than at B1, where light and flushing strongly influenced the phytoplankton community (Stockner et al. 1977).

Commencement of the spring phytoplankton bloom in the Burrard Inlet system was related to the onset of thermal stratification, high nutrient levels, and increased incident radiation ($>502\ J \cdot cm^{-2} \cdot d^{-1}$). These conditions prevailed by mid-March or early April and led to the attainment of maximum biomass by mid-May or early June at most stations. The phytoplankton community was typically coastal marine, with diatoms abundant and species composition similar to that described by Marshall (1976) and Platt and Rao (1970) on the Atlantic coast, Sakshaug (1976) and Sakshaug and Myklestad (1973) on Norwegian fiords, and by Olsson and Ölundh (1974) and Bjørn-Rasmussen (1976) in Swedish fiords.

In most situations, nitrate and ammonia concentrations limit phytoplankton growth in British Columbia coastal marine waters for reasons related to supply and regeneration (Strickland 1958; Antia et al. 1963). Phosphorus was always in excess of phytoplankton requirements and was supplied abundantly to Burrard Inlet from land drainage and effluent discharges to Port Moody Arm (Waldichuk 1965). Silicate varied in proportion to the standing stock of diatoms in spring and autumn but never reached levels considered limiting to diatoms in the marine environment (Paasche 1973a).

In the fifties and sixties, Vancouver Harbor was the receiving water for the majority of sewage and storm sewer drainage from the metropolitan area of Vancouver (S. Vernon, Greater Vancouver Regional District, personal communication). Unfortunately, no biological studies, with the exception of Waldichuk's (1965) in Port Moody Arm, were done during this period of high nutrient loading to document the impact on the biocenosis of the harbor and outer Burrard Inlet. By 1974, practically all sewers had been diverted to primary sewage treatment plants at Annacis and Iona islands in the Fraser River. This diversion has led to high nutrient levels in the Fraser River and resulted in substantial increases in primary production in surface waters of the Strait of Georgia affected by the Fraser River plume (J. G. Stockner unpublished data).

Dissolved oxygen data from Port Moody Arm gathered during the present study is similar to earlier data (Waldichuk 1965), indicating that little eutrophication and subsequent environmental degradation has occurred over the last decade, despite some increase in population in the Port Moody area. Unless nitrogen levels increase from present levels, or tidal circulation patterns are altered by geothermal power generation, Vancouver Harbor should in the future remain relatively clean and pollution-free.

Our mean annual estimates of primary production for the Burrard Inlet system ($350\ g\ C \cdot m^{-2}$) are similar to Riley's (1956) value for Long Island Sound ($380\ g\ C \cdot m^{-2}$) and estimates by Malone (1976) and Mandelli et al. (1970) for the apex of the New York Bight (370 and $420\ g\ C \cdot m^{-2}$), but lower than the value given by Winter et al. (1975) for the central basin of Puget

Sound in Washington State (465 g C·m^{-2}).

By virtue of its location on the foreshore of the Burrard Inlet system, Vancouver Harbor can be considered clean and only moderately productive because of the strong tidal flushing, moderate light climate, and the overriding influence of the estuarine circulation pattern on phytoplankton population dynamics. This is in strong contrast to other marine embayments or estuaries situated close to large population centers (Ryther and Dunstan 1971; Halim et al. 1976; Bjørn-Rasmussen 1976; Malone 1977; Sakshaug 1976; Taslakian and Hardy 1976).

Acknowledgments

We are grateful to Mr S. Matheson of the M.V. *Active Lass* for field assistance on cruises and to Messrs K. Shortreed and E. MacIsaac for assistance in data collation.

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1971. Standard methods for the examination of water and wastewater. 13th ed. Washington. D.C. 769 p.

Antia, N. J., C. D. McAllister, T. R. Parsons, K. Stephens, and J. D. H. Strickland. 1963. Further measurements of primary production using a large-volume plastic sphere. Limnol. Oceanogr. 8: 166–183.

Bjørn-Rasmussen, S. 1976. The influence of pollution on the phytoplankton in the estuary of the Göta River (Göteborg). I. The ecological situation before treatment of the wastewater, p. 145–152. *In* S. Skneslet et al. [ed.], Fresh water on the sea. Assoc. Nor. Oceanogr., Oslo, Norway.

Buchanan, R. J. 1966. A study of the species composition and ecology of the phytoplankton of a British Columbia inlet. Ph.D. Thesis. Univ. of British Columbia, Vancouver, B.C. 268 p.

Carter, N. M. 1934. The oceanography of the fiords of southern British Columbia. Fish. Res. Board Can. Pac. Prog. Rep. 12: 7–11.

Fisheries/Environmental Protection Service. 1974. Laboratory manual. Dep. Fish Environ., Fish. Mar. Serv., Pac. Reg. 180 p.

Gilmartin, M. 1962. Annual cyclic changes in the physical oceanography of a British Columbia fiord. J. Fish. Res. Board Can. 19: 921–974.

1964. The primary production of a British Columbia fiord. J. Fish. Res. Board Can. 21: 505–538.

Halim, Y., A. Samaan, and F. Zaghloul. 1976. Estuarine plankton of the Nile and the effect of fresh-water phytoplankton, p. 153–164. *In* S. Skneslet et al. [ed.], Fresh water on the sea. Assoc. Nor. Oceanogr., Oslo, Norway.

LeBrasseur, R. J. 1954. The physical oceanographic factors governing the plankton distribution in the British Columbia inlets. M.Sc. Thesis. Univ. of British Columbia, Vancouver, B.C.

Malone, T. C. 1976. Phytoplankton productivity in the apex of the New York Bight: Environmental regulation of productivity/chlorophyll *a*. Am. Soc. Limnol. Oceanogr. Spec. Symp. 2: 260–272.

1977. Environmental regulation of phytoplankton productivity in the lower Hudson estuary. Estuarine Coastal Mar. Sci. 5: 157–171.

Mandelli, E. P., P. R. Burkholder, T. E. Doheny, and R. Brady. 1970. Studies of primary productivity in coastal waters of southern Long Island, New York. Mar. Biol. 7: 156–160.

Marshall, H. G. 1976. Phytoplankton distribution along the eastern coast of the U.S.A. I. Phytoplankton composition. Mar. Biol. 38: 81–89.

Olsson, I., and E. Ölundh. 1974. On plankton production in Kungsbacka fiord, an estuary on the Swedish west coast. Mar. Biol. 24: 17–28.

Paasche, E. 1973a. Silicon and the ecology of marine plankton diatoms. I. *Thalassiosira pseudonana* (*Cyclotella nana*) grown in a chemostat with silicate as limiting nutrient. Mar. Biol. 19: 117–126.

1973b. Silicon and the ecology of marine plankton diatoms. II. Silicate-uptake kinetics in five diatom species. Mar. Biol. 19: 262–269.

Parsons, T. R., R. J. LeBrasseur, J. D. Fulton, and O. D. Kennedy. 1969b. Production studies in the Strait of Georgia, II. Secondary production under the Fraser River plume, February to May, 1967. J. Exp. Mar. Biol. Ecol. 3: 39–50.

Parsons, T. R., K. Stephens, and R. J. LeBrasseur. 1969a. Production studies in the Strait of Georgia, I. Primary production under the Fraser River plume, February to May, 1967. J. Exp. Mar. Biol. Ecol. 3: 27–38.

Platt, T., and D. V. Subba Rao. 1970. Primary production measurements on a natural plankton bloom. J. Fish. Res. Board Can. 27: 887–899.

Riley, G. A. 1956. Oceanography of Long Island Sound, 1952–1954. IX. Production and utilization of organic matter. Bull. Bingham Oceanogr. Collect. XV: 324–343.

Ryther, J. H., and W. M. Dunstan. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science 171: 1008–1013.

Sakshaug, E. 1976. Dynamics of phytoplankton blooms in Norwegian fjords and coastal waters, p. 139–144. *In* S. Skneslet et al. [ed.], Fresh water on the sea. Assoc. Nor. Oceanogr., Oslo, Norway.

Sakshaug, E., and S. Myklestad. 1973. Studies on the phytoplankton ecology of the Trondheimsfjord. III. Dynamics of phytoplankton blooms in relation to environmental factors, bioassay experiments and parameters for the physiological state of the populations. J. Exp. Mar. Biol. Ecol. 11: 157–188.

Steemann-Nielsen, E. 1952. The use of radioactive carbon (^{14}C) for measuring organic production in the sea. J. Cons. 18: 117–140.

Stockner, J. G., and D. D. Cliff. 1976. Phytoplankton succession and abundance in Howe Sound, British Columbia: a coastal marine embayment-fiord under stress. Fish. Mar. Serv. Res. Dev. Tech. Rep. 658: 32 p.

Stockner, J. G., D. D. Cliff, and D. B. Buchanan. 1977. Phytoplankton production and distribution in Howe Sound, British Columbia: a coastal marine embayment-fiord under stress. J. Fish. Res. Board Can. 34: 907–917.

Strickland, J. D. H. 1958. Data record and discussion. A special B.C. coastal survey measuring chemical and light attenuation properties, June to July 1958. MS Rep. Series (Oceanogr. Limnol.) 30: 48 p.

1960. Measuring the production of marine phytoplankton. Bull. Fish. Res. Board Can. 122: 172 p.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167: 311 p.

TABATA, S. 1971. A brief oceanographic description of the waters of Burrard Inlet and Indian Arm. MS Rep. to Mar. Sci. Dir., Pac. Reg., Dep. Environ. Canada: 48 p.

TAKAHASHI, M., K. FUJII, AND T. R. PARSONS. 1973. Simulation study of phytoplankton photosynthesis and growth in the Fraser River estuary. Mar. Biol. 19: 102–116.

TASLAKIAN, M. J., AND J. T. HARDY. 1976. Sewage nutrient enrichment and phytoplankton ecology along the central coast of Lebanon. Mar. Biol. 38: 315–325.

UTERMÖHL, H. 1958. Für Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitt. Int. Ver. Limnol. 9: 1–38.

WALDICHUK, M. 1957. Physical oceanography of the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 14: 321–486.

1965. Water exchange in Port Moody, British Columbia, and its effect on waste disposal. J. Fish. Res. Board Can. 22: 801–822.

WALDICHUK, M., J. R. MARKERT, AND J. H. MEIKLE. 1968a. Fraser River estuary, Burrard Inlet, Howe Sound and Malaspina Strait physical and chemical oceanographic data, 1957–1966. Volume I, September 1957 to February 1962. Fish. Res. Board Can. MS Rep. 939: 244 p.

1968b. Fraser River estuary, Burrard Inlet, Howe Sound and Malaspina Strait physical and chemical oceanographic data, 1957–1966. Volume II, September 1962 to July 1966. Fish. Res. Board Can. MS Rep. 939: 277 p.

WINTER, D. F., K. BANSE, AND G. C. ANDERSON. 1975. The dynamics of phytoplankton blooms in Puget Sound, a fiord in the Northwestern United States. Mar. Biol. 29: 136–176.

An Automated Device (AGARS) for Studying Avoidance of Pollutant Gradients by Aquatic Organisms[1]

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CRIPE, C. R. 1979. An automated device (AGARS) for studying avoidance of pollutant gradients by aquatic organisms. J. Fish. Res. Board Can. 36: 11–16.

Most apparatus designed to detect avoidance of pollutants by aquatic organisms require visual observations of test organisms in steep pollutant gradients. AGARS (Aquatic Gradient Avoidance Response System) was developed to eliminate these limitations. This system allows animals to choose between one uncontaminated zone and three increasingly toxic zones in a gradient trough that is monitored for extended time periods by infrared light sources, sensors, and a microprocessor. Data are accumulated hourly and processed by a paper tape reader/calculator/plotter system that records the time test animals remain in each zone and compares behavior before and during test exposures. Initial tests indicate that pinfish (*Lagodon rhomboides*) tested in the apparatus will avoid chlorine-produced oxidants at concentrations of 0.02–0.04 mg/L.

Key words: avoidance responses, behavioral bioassays, automated monitoring systems, chlorine-produced oxidants

CRIPE, C. R. 1979. An automated device (AGARS) for studying avoidance of pollutant gradients by aquatic organisms. J. Fish. Res. Board Can. 36: 11–16.

La plupart des appareils servant à détecter l'évitement des contaminants par les organismes aquatiques requièrent l'observation visuelle des organismes expérimentaux dans des gradients prononcés de contaminants. Nous avons mis au point un système, l'AGARS (« Aquatic Gradient Avoidance Response System »), qui n'est pas soumis à ces contraintes. Grâce à ce système, les animaux peuvent choisir entre une zone non contaminée et trois zones de toxicité croissante dans un bassin à gradient pouvant être surveillé durant de longues périodes à l'aide de sources de lumière infrarouge, de détecteurs et d'un organe de micro-traitement. Les données sont accumulées d'heure en heure et traitées au moyen d'un système comprenant un lecteur de bande perforée, une calculatrice et un traceur, qui enregistre le temps passé par les animaux expérimentaux dans chaque zone et qui compare leur comportement avant et durant les expériences. Des essais préliminaires indiquent que des *Lagodon rhomboides* placés dans l'appareil évitent des oxydants produits par le chlore à des concentrations de 0,02 à 0,04 mg/L.

Received April 5, 1978
Accepted October 11, 1978

Reçu le 5 avril 1978
Accepté le 11 octobre 1978

THE avoidance of pollutants by fish and invertebrates can cause their absence from the pollutant source (Sprague et al. 1965; Fava and Tsai 1976; Laughlin et al. 1978). Lack of avoidance could result in the death of an organism or bioconcentration of harmful substances. Laboratory tests that determine an organism's threshold of avoidance or preference for a pollutant can thus be an aid in determining the impact of the pollutant. The adaptive significance of fish locomotor orientation behavior and approaches to quantifying and forecasting responses to environmental stimuli (i.e. temperature, light, or chemicals) have been addressed by Kleerekoper (1977).

Most avoidance tests involve the visual observation of animals during daylight hours, for less than 30 min, in Y-shaped troughs (Laughlin et al. 1978), rectangular troughs (Lewis and Livingston 1977), or cylinders (Middaugh et al. 1977a). Short-term visual monitoring may not provide information about long-term exposure. Long-term observations might reveal that organisms acclimate to a toxicant or react differently to a pollutant in darkness. For example, a pollutant's turbidity (Lawrence and Scherer 1974) or difference in color from the surrounding water may not be detected by organisms in darkness.

Most avoidance tests present a very steep gradient, rather than the shallow gradient likely to occur in the field. Several investigators have indicated that the response to steep and shallow toxicant gradients are not always the same (Timms and Kleerekoper 1972; West-

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Printed in Canada (J5204)
Imprimé au Canada (J5204)

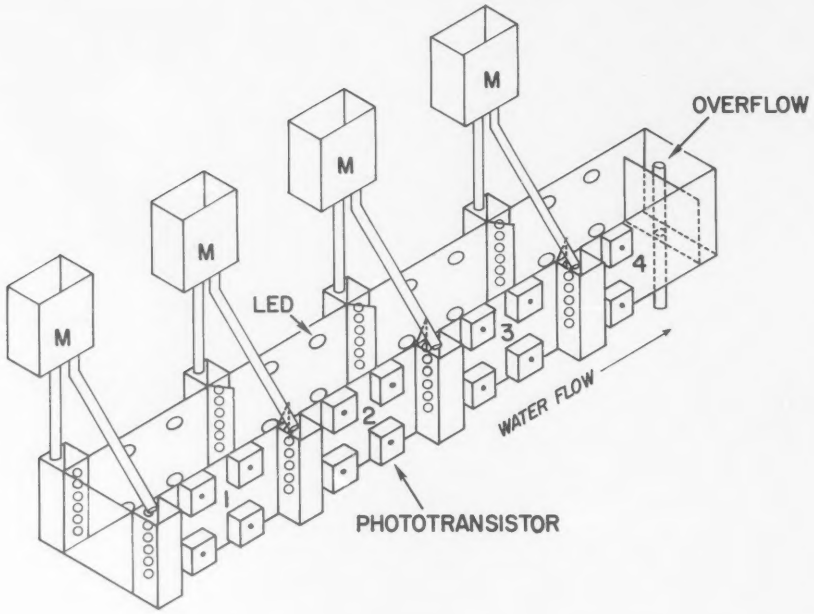

FIG. 1. Diagram of AGARS (Aquatic Gradient Avoidance Response System) trough; for a full description of dimensions see text. Organism position can be monitored in both the upper and lower half of each area (1–4) by pairs of infrared light-emitting diodes (LEDs) and phototransistors.

lake and Kleerekoper 1974). Results have usually been obtained by testing water with one pollutant concentration vs. water free of the pollutant, requiring a series of tests to establish a threshold avoidance concentration.

A system described by Kleerekoper et al. (1970) solves some of these problems. It monitors the orientation of test organisms to pollutant gradients in a 5-m square tank with 1936 photoconductive cells and an on-line computer. This method, however, is expensive. In addition, its light sources (at a color temperature of 2400°) would radiate a significant amount of visible light (Koller 1952) which may affect nocturnal activity patterns. Thus, the need exists for a relatively inexpensive system that produces a gradient, functions automatically, and is easily operated.

The system described here, an Aquatic Gradient Avoidance Response System (AGARS), produces a pollutant gradient in a continuous-flow system, providing the test animal with a choice between uncontaminated water and three pollutant concentrations in a rectangular trough. The position of the organism in the trough is monitored by infrared lights (peak emission 940 nm, range 860–1060 nm) to avoid affecting the organism's photoperiod response; sensors are scanned at preset intervals by an inexpensive microprocessor. Cumulative data, periodically punched on paper tape by a teletypewriter, can be analyzed manually or by calculators or computers equipped with a tape reader. Thus, a relatively large amount of data on avoidance behavior can be manipulated, avoiding the cost of an expensive on-line computer. Results of a test with a chlorine-produced oxidant gradient illustrates the advantages of a system that eliminates the need for visual observations and steep gradients.

Materials and Methods

The gradient trough (Fig. 1) is constructed of clear 6-mm plexiglass with inner dimensions of 125 × 17 × 15 cm high. A peristaltic pump injects a test compound and carriers, when required, into a continuous supply of 1.5 L of seawater/min before flowing into plexiglass mixing boxes. Mixing is accomplished through turbulence. This flow is divided evenly between pairs of small chambers along opposite sides of the gradient trough. Water enters the main trough area through a vertical row of six 7-mm holes designed to control water flow. Vertical strips of plexiglass (at a 45° angle to the side of the trough) channel incoming water toward the drain. Water flow maintains a gradient consisting of a control zone and zones that receive three increasing toxicant concentrations. By adding increasing

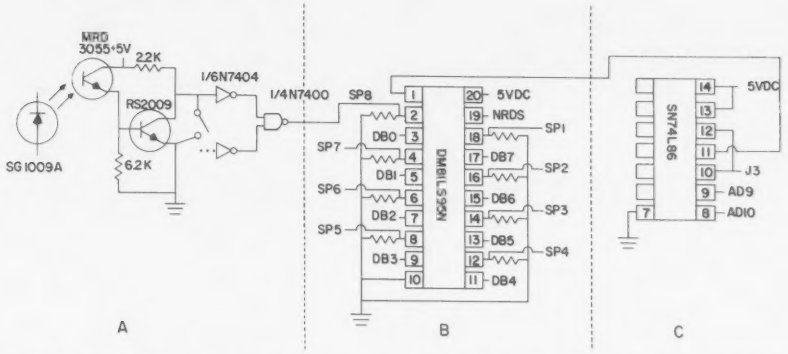

FIG. 2. Diagram of circuits for monitoring positions of organisms within gradient trough: A, Phototransistor circuit; B, Octal buffer circuit; C, IC circuit for addressing octal buffer. SP1–8 represent the digitalized outputs from the eight sensor pairs in Part A. DBØ-7, NRDS, and AD 9–10 are connected to the corresponding pins of the microprocessor chip. J3 is marked on the microprocessor printed circuit board. The eight resistors in B are 10K, ¼ W.

toxicant concentrations to Areas 1–4, the gradient increases as it flows downstream. To reverse the gradient, toxicant addition to Area 1 produces a gradient that decreases downstream due to dilution with clean water from Areas 2 to 4. The same organisms can be subjected to both gradients on different days to eliminate possible bias due to end effects or rheotaxis.

An opaque, plastic curtain, enclosing the gradient trough, eliminates visual disruptions. Photoperiods are maintained by a timer (12L:12D) controlling two 40-W fluorescent lights. Filtered seawater is temperature-controlled and its salinity is monitored. Animals are fed frozen adult brine shrimp (free from significant PCB or common organochlorine pesticide residues) at irregular intervals through tubes that penetrate the plastic curtain, thus preventing anticipation of food. Food enters the trough at three points between each of the four areas. Animals are normally not fed during the 24-h period when a toxicant gradient is present. Water is sampled from the centers of the four areas for analysis using a glass siphon with a Teflon® stopcock. Each area's siphon normally rests near the surface and is gently lowered from outside the plastic curtain to the center of the trough to take a sample.

The position of the organism in the trough indicates preference for a point in the gradient. By separating the upper and lower areas within the same concentration zone, other behavioral changes such as surface swimming of benthic organisms can be observed. The position of test animals in the upper or lower zones in the four areas is determined by the interruption of two pairs of infrared light beams and phototransistors per zone. A slightly modified version of previously described circuitry (Cripe et al. 1975) is used for the sensing system. AGARS uses RCA SG1009A infrared light-emitting diodes (LEDs) as light sources. The detector circuit (Fig. 2A) combines the signals from two sensors monitoring the same one-eighth area of the trough. An SN7440 integrated circuit (IC) could be used in place of the SN7400 to integrate the signal from all four sensors in the same concentration zone (the SN7400 monitors one pair of sensors in upper or lower half of area).

AGARS data are processed as follows. The status of the eight pairs of sensors is scanned by an inexpensive ($99) SC/MP microprocessor (National Semiconductor, ISP-SK/200) at 0.33-s intervals to determine the time and position of animals in the light beams. An animal resting in front of the beam continues to add to the cumulative time in the area. Cumulative results are sent hourly to a teletypewriter (Teletype Corp. Model 3320/3JC) that records totals in hexadecimal on a punched paper tape. Tape data are entered in a calculator/tape reader/X–Y plotter system (Hewlett Packard, Models 9825A, 2748B, and 9862A, respectively) and converted to decimal. Time spent in each zone is plotted, and results are analyzed statistically by a *t*-test corrected for uneven variance.

The basic SC/MP microprocessor is modified slightly for monitoring the sensors (Fig. 2). The jumper between J3 and J4 on the printed circuit board is broken. J3 is connected to an output of an SN74L86 gate (Fig. 2C); the eight bits of data from the trough are interfaced with an octal buffer, DM81LS95 (Fig. 2B). The ICs and resistors (Fig. 2B and C) fit in vacant predrilled holes on the printed circuit board. A program that scans eight pairs of sensors every 0.33 s and types hourly totals can be provided on request.

All 16 LEDs are wired in series to a 24 VDC power supply with a 300-ohm, 25-W, variable resistor in series to limit the current to approximately 40 mA. The sensor system requires a regulated +5 VDC power supply; the microprocessor needs both +5 VDC and −12 VDC. Three rechargeable lead–acid storage batteries (12V, 84 A·h) are used to supply power to the voltage regulators for the microprocessor so that possible loss of microprocessor memory, in event of power failure, is eliminated.

INITIAL AVOIDANCE STUDIES

Pinfish, (*Lagodon rhomboides*), SL = 6.5 cm, were seined from Santa Rosa Sound, Florida, near the Gulf

Breeze Environmental Research Laboratory. The pinfish were held in flowing, filtered seawater (22.7°–30.2°C, salinity 22–24‰) for 12 d before testing in AGARS.

The toxicant tested for avoidance was sodium hypochlorite, estimated as chlorine-produced oxidants (CPO) by amperometric titration with phenylarsine oxide buffered at a pH of 4.0. Stock solutions (distilled water and three sodium hypochlorite solutions at nominal concentrations of 310, 2100, and 3700 mg/L CPO) were metered into the four mixing boxes, Areas 1–4, respectively, at 1.0 mL/min by a Harvard Model 1203 Peristaltic Pump and silicone tubing. To determine concentration variability within each of the four areas, a gradient was established and water samples were analyzed from different points in each area over a period of several hours. Six points in Area 1, and 11 points in Areas 2–4, were sampled. CPO concentrations (milligrams per litre, mean ± SD) expected and found were as follows:

	Area			
	1	2	3	4
CPO expected	0.00	0.10	0.53	1.03
CPO found	0.00	0.02	0.09	0.28
	±0.00	±0.01	±0.03	±0.04

Four pinfish were monitored in the trough and time spent in each area was recorded for 9 d. Triplicate 200-mL samples were siphoned twice from the center of the four areas during each 24-h avoidance gradient exposure period. No toxicant was present on Days 1–3, 5, 6, 8, and 9. On Day 4 the gradient increased downstream and on Day 7 the gradient decreased downstream by addition of CPO in Area 1 only and by diluting with clean water in Areas 2–4. CPO concentrations (mg/L, mean ±SD) expected and found on Days 4 and 7 were as follows:

		Area			
Day		1	2	3	4
4	CPO expected	0.00	0.10	0.53	1.03
	CPO found	0.00	0.02	0.07	0.21
		±0.00	±0.01	±0.02	±0.03
7	CPO expected	0.52	0.26	0.17	0.13
	CPO found	0.09	0.04	0.02	0.01
		±0.01	±0.01	±0.00	±0.00

Trough temperatures during the 9-d test were between 28.5° and 29.0°C; salinity ranged from 22 to 26‰.

Avoidance response was determined by a t-test corrected for uneven variance on data from each area for a 24-h period, as compared with the distribution on the preceding day. An α level of 0.05 was used to determine significant decreases in time spent in an exposure area.

Results and Discussion

Both tables above indicate a substantial difference between expected and observed CPO values. This initial loss of CPO during chlorination of water is due to chlorine demand, and results from reaction with easily oxidized organic compounds, ferrous ions, sulfides, nitrites, and other reducing agents (Johnson 1978).

No CPO was added during the first 3 d of the test when fish were acclimated to the device (Fig. 3). On Day 1 fish spent most of the time in Area 1 where the current was the lowest. On Days 2 and 3 fish were distributed more uniformly throughout the four areas.

After CPO was added to the water on Day 4, pinfish spent significantly ($\alpha \leq 0.05$) less time than during the preceding day in Areas 3 (0.07 mg/L) and 4 (0.21 mg/L) where CPO concentrations were highest. No avoidance of Area 2 (0.02 mg/L) was evident. More residence time was recorded in Area 1 (control area) on Day 4, probably due to the avoidance of Areas 3 and 4. The avoidance threshold was thus indicated to be between 0.07 and 0.02 mg/L. Return to CPO-free water on Days 5 and 6 resulted in a continued high presence in Areas 1 and 2.

On Day 7, the second toxicant exposure day, Areas 1 (0.09 mg/L) and 2 (0.04 mg/L) were significantly ($\alpha \leq 0.05$) avoided; no avoidance was shown in Area 3 (0.02 mg/L), and an increased presence was recorded in Area 4 (0.01 mg/L), indicating a fish avoidance threshold of approximately 0.02 to 0.04 mg/L CPO. For Days 8 and 9 (CPO-free) fish spent more time in Area 4 than in any other area.

For 2 d following each toxicant exposure, fish continued to spend more time in the end that they had previously selected, perhaps indicating a conditioned response. This behavior was apparently overcome by reversing the gradient and does not appear to affect the usefulness of the apparatus. Total time spent in the light beams per hour is not fixed, since at any instant 0–4 light beams may be interrupted depending on the position of each of the four fish. Total time decreased on both exposure days and then increased on successive toxicant-free days. The reason for this was not determined but may be the result of toxicant-induced behavioral modifications such as decreased schooling size or decreased swimming activity.

Few data are available on avoidance thresholds for fish under saltwater conditions. Middaugh et al. (1977b) found that juvenile spot (*Leiostomus xanthurus*) tested at 19–22‰ avoided a total residual chlorination (TRC) of 0.05 mg/L at 15° and 20°C. No avoidance was observed at 0.03 mg/L (D. P. Middaugh, U.S. EPA Laboratory, Bears Bluff Field Station, P.O. 368, Johns Island, S.C. 29455, personal communication) at either 15° or 20°C; the avoidance threshold, 0.05–0.03 mg/L, was near the incipient LC50 level of 0.06 mg/L TRC. This threshold appears consistent with the range of 0.02–0.04 mg/L for pinfish in my AGARS test.

These data demonstrate the applicability of AGARS in examining an organism's long-term continuous avoidance of a pollutant. The versatility of the system, combined with the elimination of visual monitoring, presents advantages over other methods mentioned. The dimensions of the system place certain locomotor restrictions on the test organisms, as well as on their

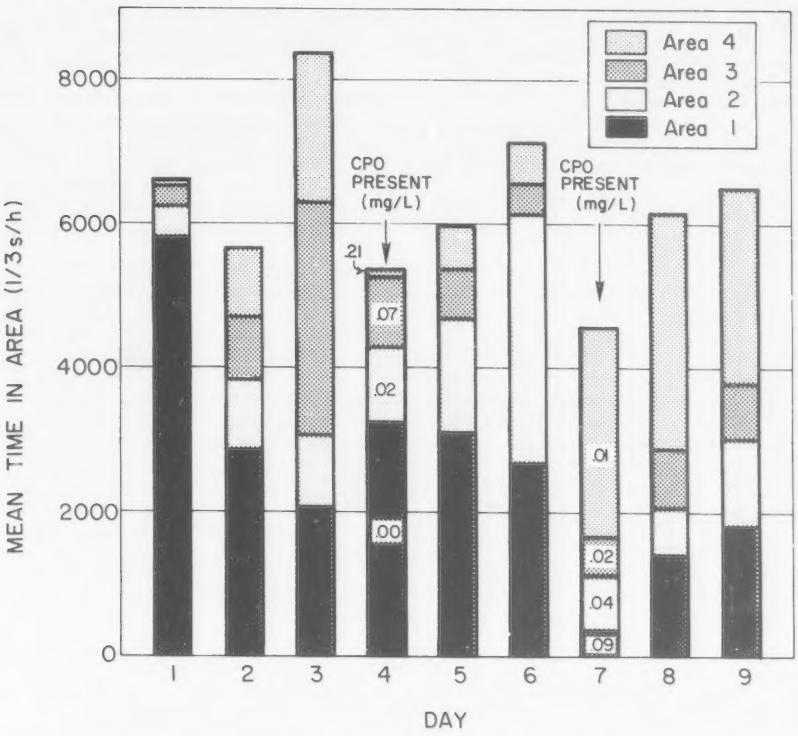

FIG. 3. Results of 9-d AGARS test with a group of four pinfish. Mean of 24-h totals of time spent in each of four areas of trough vs. elapsed time of test. On Days 1–3, 5, 6, 8, and 9 no toxicant was present. Chlorine produced oxidants (CPO) were present on Days 4 and 7. Mean CPO values are shown for two sampling periods per 24 h, with three replicates per sampling period.

maximum size. The system is a prototype, however, and can be enlarged by using more powerful lights and greater microprocessor memory capacity. In addition to several species of fish, baseline data have also been obtained with blue crabs, *Callinectes sapidus*, and penaeid shrimp. This system could also be used to test thermal or salinity preferences, provided the gradient is not so steep as to allow stratification of differing densities.

Acknowledgment

I wish to thank S. Foss for preparing the illustrations.

CRIPE, C. R., J. H. CRIPE, AND R. J. LIVINGSTON. 1975. Apparatus for the quantitative determination of locomotor activity patterns of aquatic organisms using infrared light-emitting diodes. J. Fish. Res. Board Can. 32: 1884–1886.

FAVA, J. A., AND C. TSAI. 1976. Immediate behavioral reactions of blacknose dace, *Rhinichthys atralutus*, to domestic sewage and its toxic constituents. Trans. Am. Fish. Soc. 105: 430–441.

JOHNSON, D. J. 1978. Measurement and persistence of chlorine residuals in natural waters, p. 4. *In* R. L. Jolley [ed.] Water Chlorination: Environmental Impact and Health Effects. Vol. 1. Ann Arbor Science. Ann Arbor, Mich.

KLEEREKOPER, H. 1977. Some monitoring and analytical techniques for the study of locomotor responses of fish to environmental variables, p. 110–120. *In* J. Cairns Jr., K. L. Dickson, and G. F. Westlake [eds.] Biological Monitoring of Water and Effluent Quality, ASTM STP 607, American Society for Testing and Materials. Philadelphia, Pa.

KLEEREKOPER, H., A. M. TIMMS, G. F. WESTLAKE, F. B. DAVY, T. MALAR, AND V. M. ANDERSON. 1970. An analysis of locomotor behavior of goldfish (*Carassius auratus*). Anim. Behav. 18: 317–330.

KOLLER, L. R. 1952. Ultraviolet radiation. John Wiley and Sons, Inc., New York, N.Y. p. 90–105.

LAUGHLIN, R. A., C. R. CRIPE, AND R. J. LIVINGSTON. 1978. Field and laboratory avoidance reactions by blue crabs (*Callinectes sapidus*) to storm water runoff. Trans. Am. Fish. Soc. 107: 78–86.

LAWRENCE, M., AND E. SCHERER. 1974. Behavioral responses of whitefish and rainbow trout to drilling fluids. Fish.

Mar. Serv. Res. Dev. Tech. Rep. 502: 47 p.

LEWIS, F. G., III, AND R. J. LIVINGSTON. 1977. Avoidance of bleached kraft pulpmill effluents by pinfish (*Lagodon rhomboides*) and gulf killifish (*Fundulus grandis*). J. Fish. Res. Board Can. 34: 568–570.

MIDDAUGH, D. P., J. A. COUCH, AND A. M. CRANE. 1977a. Responses of early life history stages of the striped bass, *Morone saxatilis*, to chlorination. Chesapeake Sci. 18: 141–153.

MIDDAUGH, D. P., A. M. CRANE, AND J. A. COUCH. 1977b. Toxicity of chlorine of juvenile spot, *Leiostomus xanthurus*. Water Res. 11: 1089–1096.

SPRAGUE, J. B., P. F. ELSON, AND R. L. SAUNDERS. 1965. Sublethal copper–zinc pollution in a salmon river — a field and laboratory study. Int. J. Air Water Pollut. 9: 531–543.

TIMMS, A. M., AND H. KLEEREKOPER. 1972. Locomotor response of goldfish, channel catfish, and largemouth bass to a 'copper-polluted' mass of water in an open field. Water Resour. Res. 8: 1574–1580.

WESTLAKE, G. F., AND H. KLEEREKOPER. 1974. The locomotor response of goldfish to a steep gradient of copper ions. Water Resour. Res. 10: 103–105.

Characterization of Particulate Organic Matter Transported by Some Cascade Mountain Streams

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NAIMAN, R. J., AND J. R. SEDELL. 1979. Characterization of particulate organic matter transported by some Cascade Mountain streams. J. Fish. Res. Board Can. 36: 17–31.

Field and laboratory studies were conducted to characterize concentrations, factors determining concentrations, particle size composition, and presumed food quality of particulate organic matter (POM) transported by streams of four different orders in Oregon's Cascade Mountains. Devils Club Creek (first order) and Mack Creek (third order) as high gradient, heavily shaded headwater streams receive large amounts of forest debris. Lookout Creek (fifth order) and the McKenzie River (seventh order) have lower gradients and more organic inputs from in situ aquatic primary producers and organic matter drifting from upstream areas than from the adjacent forest. Concentration of particulate organic matter is low during periods of nonstorm discharge, and not significantly related to stream power or type of organic input. All streams transport a mean POM particle size <12 μm. Over 70% of all particulate organic matter transported is very fine particulate organic matter (VPOM: 0.45–53 μm). Except for spring, the ratio of coarse (>1 mm) to fine (0.45 μm–1 mm) organic matter (CPOM:FPOM) is near zero, but remains elevated for the McKenzie River during all seasons. As determined by the amount of chlorophyll, carbon to nitrogen (C:N) ratio, percentage of organic matter and respiration rate, the presumed food quality of drifting organic matter is potentially better in downstream reaches.

Key words: food quality, detritus, organic matter, streams, rivers, watershed, drift, transport

NAIMAN, R. J., AND J. R. SEDELL. 1979. Characterization of particulate organic matter transported by some Cascade Mountain streams. J. Fish. Res. Board Can. 36: 17–31.

On a fait des études sur le terrain et au laboratoire dans le but de déterminer les concentrations, les facteurs responsables de ces concentrations, la grosseur des particules et la qualité nutritive présumée de matériaux organiques particulaires (POM) transportés par des cours d'eau de quatre ordres différents dans les montagnes Cascades de l'Orégon. Le ruisseau Devils Club (premier ordre) et le ruisseau Mack (troisième ordre), cours d'eau à gradient prononcé et à tête très ombragée, reçoivent de grandes quantités de débris forestiers. Le ruisseau Lookout (cinquième ordre) et la rivière McKenzie (septième ordre) ont des gradients moins prononcés et reçoivent de plus grands apports de matière organique des producteurs primaires aquatiques *in situ* et de matière organique dérivante en provenance des régions d'amont qu'ils n'en reçoivent de la forêt avoisinante. La concentration de matières organiques particulaires est basse durant les périodes de débit autres que les débits d'orages, et n'est pas nettement liée à la force du cours d'eau ou au type d'apport organique. Tous les cours d'eau transportent des POM de grosseur inférieure à 12 μm. Plus de 70% de toute la matière organique particulaire transportée est une matière particulaire très fine (VPOM : 0,45 à 53 μm). Sauf au printemps, le rapport des matières organiques grossières (>1 mm) aux matières fines (0,45 μm à 1 mm) (CPOM:FPOM) se rapproche de zéro, mais demeure élevé dans la rivière McKenzie à toute saison. A en juger par la quantité de chlorophylle, le rapport carbone:azote (C:N), le pourcentage de matières organiques et le taux de respiration, la qualité nutritive présumée des matières organiques dérivantes est potentiellement supérieure dans la partie inférieure des cours d'eau.

Received July 27, 1978
Accepted October 12, 1978

Reçu le 27 juillet 1978
Accepté le 12 octobre 1978

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Printed in Canada (J5322)
Imprimé au Canada (J5322)

TRANSPORT of organic detritus by streams and rivers is a conspicuous component of their ecosystem structure but has never been adequately characterized for potential food quality, relative proportions of size fractions, or basic differences inherent between stream orders in a given watershed. Transport of organic detritus in streams and rivers is important to invertebrates, especially the filter feeders (Cummins 1974; Wallace et al. 1977), and can be of considerable significance to estuarine communities (Naiman and Sibert 1978). By contrast, drift of living organisms in streams is better documented (Waters 1969).

Studies of drifting organic detritus have been mostly concerned with concentrations of the dissolved (<0.45 μm) and particulate (>0.45 μm) fractions, and only a few studies address an entire year (Fisher and Likens 1973; Hobbie and Likens 1973; Brinson 1976; Naiman 1976; Liaw and MacCrimmon 1977). Other studies have microscopically examined downstream variations in the structure of drifting organic detritus (Egglishaw and Shackley 1971), while the origin and fate of plankton in streams has been examined by Chandler (1937), Maciolek and Tunzi (1968), and Swanson and Backmann (1976). The role of filter feeders in streams, and their food, was recently reviewed by Wallace et al. (1977). Seki et al. (1969), Stephens et al. (1967), and Naiman and Sibert (1978) studied the importance and fate of stream inputs of organic material to coastal environments. Vannote has theorized on the ratio of coarse to fine organic detritus in relation to stream order (Cummins 1975, 1977), but only Sedell et al. (1979) have attempted to relate concentrations to physical factors.

In this paper we characterize drifting organic detritus in four streams of different order in Oregon's Cascade Mountains. We examine by size fraction, concentrations, percentage organic matter, carbon to nitrogen (C:N) ratio, chlorophyll *a*, and respiration rate. We test the hypothesis that coarse particulate organic matter (CPOM: >1 mm) is not an important component of drifting organic matter in very small (first order) streams, becomes increasingly important in slightly larger (second–third order) streams where greater power is available to move larger particles, and then decreases in importance in larger streams as abiotic–biotic processing is completed (Cummins 1975, 1977). We also attempt to relate concentrations of particulate organic matter (POM) to unit stream power and presence of retention structures. Finally, we examine the postulate that the overall food quality of drifting organic matter is better in downstream reaches.

Study Area

The H. J. Andrews Experimental Forest (6000 ha, 60 km²) in Oregon's Cascade Mountains is characterized by high gradient streams, a maritime climate, and distinct seasonal rainfall. All streams experience autumn and spring freshets and low summer flows. Annual precipitation ranges from 225 cm at lower elevations to 350 cm on the ridges. High elevations have extensive snow packs during winter, while rain predominates at lower elevations (Berntsen and Rothacher 1959). Dominant forest vegetation is Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and alder (*Alnus rubra*) along the lower elevation streams. Three of the four study sites (Devils Club Creek, Mack Creek, and Lookout Creek) are within the Andrews Forest, and one (McKenzie River) is adjacent to the forest.

Devils Club Creek is a first order stream (Strahler 1957) (Table 1, Fig. 1). The stream channel is choked with coarse organic debris derived from windfall Douglas fir (≈400 yr old) accumulated over the last several hundred years, and leaf fall from huckleberry (*Vaccinium parvifolium*), devils club (*Oplopanax horridum*), maple (*Acer macrophyllum* and *Acer circinatum*), and Douglas fir needles (Naiman and Sedell unpublished data). Autochthonous production is extremely low (Naiman and Sedell unpublished data) in this heavily shaded stream which discharges directly into Mack Creek.

Mack Creek is one of three major streams draining the Andrews Forest (Table 1, Fig. 1). The morphology of this third order stream is characterized by a stairstep of gouged pools, free fall zones, and turbulent water around large boulders. Substrate ranges from large boulders to sand but is mostly loose cobble (Sedell et al. 1975). Woody debris is prevalent but much less concentrated than in Devils Club Creek. In Mack Creek the forest canopy opens slightly, allowing light flecks to reach the stream. There is some primary production by microalgae but it is still not a major organic input (Gregory 1978; Naiman and Sedell unpublished data). Windborne debris, lateral movement from steep side slopes, and downstream transport from tributaries are the primary biological inputs. Mack Creek is a major tributary of Lookout Creek.

Lookout Creek receives runoff from the entire Andrews Forest (Table 1, Fig. 1). This fifth order stream consists of shallow riffles interspersed with small pools; the substrate is large cobbles and bedrock. There is little woody debris in the stream, the canopy is open, and most daily sunlight reaches the extensive periphyton community (Naiman and Sedell unpublished data). Primary production by diatoms, filamentous algae, and stream lettuce (*Prasiola*), as well as transport from upland areas, are the major organic inputs. Allochthonous input from leaf fall is important only in late summer and autumn when maple leaves and conifer needles reach the stream. Lookout Creek discharges into Blue River which, in turn, is a tributary of the McKenzie River.

The McKenzie River is a seventh order stream draining the western Cascade Mountains (Table 1, Fig. 1). Morphologically, it is 85% riffle-runs with few alcoves or pools. Substrate is cemented cobble and large boulders; significant woody debris has not accumulated. Alder and Douglas fir along stream margins contribute some organic matter but most inputs are from downstream transport, periphyton production, and aquatic macrophytes. A zone of aquatic mosses (*Fontinalis* sp.) extends 5 m from both banks. There is a moderate to dense periphyton community over the entire substrate (Naiman and Sedell unpublished data).

Autochthonous and allochthonous inputs, the immediate sources of drifting organic matter, vary widely in amount and composition for each study site (Naiman and Sedell unpublished data). Once inputs reach the stream they have

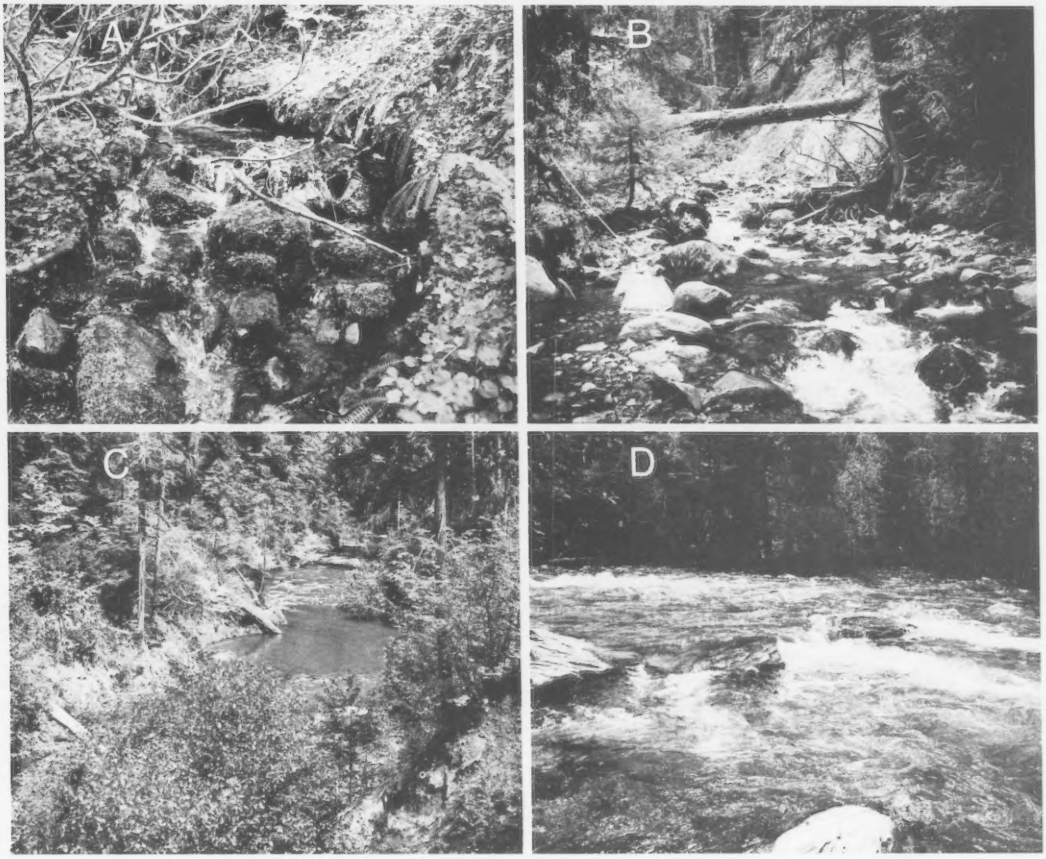

FIG. 1. A, Devils Club Creek; B, Mack Creek; C, Lookout Creek; D, the McKenzie River.

the potential to drift immediately or be retained and processed in place. Each biological input will show a different propensity for drifting and abiotic–biotic processing rates depending upon composition, temperature, water chemistry, stream flow, and stream morphometry. In general, all Andrews Forest sites have similar temperature regimes with winter lows of about 1°C and summer maxima of about 15–18°C, and similar water chemistry (Table 2). The McKenzie River, however, has a narrower temperature range varying from about 3°C in winter to 12°C in summer, and a slightly different water chemistry with higher concentrations of phosphorus, lower concentrations of nitrogen, and slightly higher alkalinity. All four sites are quite different in stream flow and morphometry (Table 1).

Materials and Methods

We sampled during periods of normal seasonal flow in March (winter), May (spring), July (summer), and October (autumn) in 1976, and in February (winter) 1977. Unusual events (freshets) were not sampled because they were judged not to be of immediate importance to the biological community, although freshets are of great importance in the redistribution of organic matter.

Organic drift $>106\ \mu m$ was estimated at all sites with Miller high speed plankton samplers. In Devils Club Creek either the entire stream was diverted through the sampler, or at high flows, a substantial portion of the stream was channeled by a hose into the net. Nets in Devils Club Creek

TABLE 1. Physical characterization of sampling locations.

Parameter	Devils Club Creek	Mack Creek	Lookout Creek	McKenzie River
Mean width (m)	0.6	3.0	12.0	40.0
Mean depth (m)	0.05	0.22	0.90	1.60
Discharge ($L \cdot s^{-1}$):				
Maximum	14.0	825	8 462	115 000
Mean Annual	1.7	92	377	75 300
Minimum	0.3	25	258	13 500
Stream gradient (%)	40.0	13.0	3.0	0.6
Watershed area (km^2)	0.2	6.0	60.5	1 024.0
Stream length (km)	0.5	3.2	14.4	57.6
Stream length / Watershed area ($km \cdot km^{-2}$)	5.00	0.72	0.22	0.06
Freshets per year				
5x Base flow	32	12	6	0
10x Base flow	13	5	2	0
Stream order	1	3	5	7
Elevation (m)	810	800	420	410
Benthic detritus ($g\ AFDW \cdot m^{-2}$)	117 677	15 393	123	84

TABLE 2. Summary of water chemistry for sampling site by season ($mg \cdot L^{-1}$). TDS = Total dissolved solids ($mg \cdot L^{-1}$).

Season	Location	Total P	Ortho P	NH_3-N	NO_2-N	NO_3-N	Total N	TDS	Hardness	Alkalinity ($mmol \cdot L^{-1}$)	Sample size (n)
Winter	Devils Club Creek	0.0361	0.0039	0.0109	0	0.0235	0.0298	42.3	9.8	0.105	3
	Mack Creek	0.0279	0.0080	0.0022	0	0.0222	0.0273	36.0	10.1	0.092	3
	Lookout Creek	0.0429	0.0096	0.0069	0	0	0.0227	30.5	9.7	0.013	2
	McKenzie River	0.0670	0.0327	0.0072	0	0	0.0072	34.5	15.3	0.190	4
Spring	Devils Club Creek	0.0231	0.0109	0.0011	0	0.0003	0.0230	50.3	12.4	0.063	4
	Mack Creek	0.0150	0.0058	0	0	0.0760	0.0295	36.3	8.2	0.056	4
	Lookout Creek	0.0261	0.0073	0.0034	0	0.0327	0.0284	36.0	8.1	0.066	4
	McKenzie River	0.0528	0.0282	0.0032	0	0.0042	0.0247	47.3	14.3	0.167	4
Summer	Devils Club Creek	0.0176	0.0120	0.0264	0	0.0006	0.0278	89.2	14.6	0.129	5
	Mack Creek	0.0150	0.0104	0.0090	0	0.0238	0.0252	87.2	11.0	0.107	5
	Lookout Creek	0.0150	0.0108	0.0059	0	0.0054	0.0272	98.2	12.4	0.131	5
	McKenzie River	0.0404	0.0342	0.0012	0	0.0010	0.0108	95.6	15.6	0.197	5
Autumn	Devils Club Creek	0.0284	0.0128	0.0265	0	0.0006	0.0298	4.9	13.9	0.137	5
	Mack Creek	0.0304	0.0124	0.0025	0	0.0034	0.0224	5.2	13.0	0.132	5
	Lookout Creek	0.0326	0.0154	0.0032	0	0.0432	0.0246	5.8	13.0	0.055	5
	McKenzie River	0.0630	0.0496	0.0011	0	0.0026	0.0044	6.5	17.0	0.244	5

TABLE 3. Average seasonal concentration (mg AFDW·m^{-3}) of drifting particulate organic matter and the diel coefficient of variation (CV, %) is calculated for each stream.

	Mean particulate transport							
	Devils Club Creek		Mack Creek		Lookout Creek		McKenzie River	
Season	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV
Winter	1347.4	13.9	1266.9	20.7	1102.8	29.3	681.9	7.6
Spring[a]	539.1	0.2	212.3	3.2	309.0	2.1	918.8	2.2
Summer	1078.5	4.3	461.6	7.7	455.9	0.9	751.3	1.4
Autumn	900.3	16.6	425.6	19.2	447.4	24.5	615.7	27.1
Mean	966.3	8.8	591.6	12.7	578.8	14.2	741.9	9.6

[a]53–106 μm not sampled.

were left in place for 4–14 h over 1–3 d each season. Organic matter transported in Mack Creek, Lookout Creek, and the McKenzie River was sampled for various times up to an hour, 4–8 times at equal intervals over a diel period for 1–3 d each season. The nets were not allowed to clog with debris.

Concentrations in milligrams AFDW per cubic metre were estimated, after any large invertebrates were removed, by dividing the ash-free dry weight (AFDW) of the sample by the estimated volume of water filtered by the nets. The volume of water sampled was determined with fluorescent dyes and is accurate to ±5%. Dyes were injected into the mouth of the sampler and the time taken to pass through recorded. These data were combined with sampler volume to estimate volume of water filtered. All material taken in the Miller sampler was sorted into size-classes of >16 mm, 16–4 mm, 4–1 mm, 1 mm–500 μm, 500–250 μm, and 250–106 μm. Concentration of particles between 53 and 106 μm was determined by filtering 200 L of water through a 53-μm screen. This was done twice in spring and 12 times over 1–3 d for other seasons for all sites. For particles in the 0.45–53-μm size fraction, 15–20 L of water was first sieved through a 53-μm net and then filtered onto a preweighed and precombusted (550°C, 2–4 h) Gelman glass fiber filter until it clogged. The total volume filtered was noted. This size fraction was estimated only 1–3 times in spring and 10–12 times, during a 1–3-d period, for the remaining seasons. For winter samples this size fraction was further subdivided into 5.0–53 μm and 0.45–5.0 μm. Water was sieved through a 53-μm net and filtered through a 5.0-μm nucleopore filter. Water passing through this filter was passed through a Gelman glass fibre filter.

To facilitate comparison with other studies we defined coarse particulate organic matter (CPOM) as particles >1 mm diam; fine particulate organic matter (FPOM) as >0.45 μm–1 mm diam; and very fine particulate organic matter (VPOM) as 0.45–53 μm (Boling et al. 1975).

The amount of material transported by streams is partially a function of stream power. Unit stream power is an indication of the ability of water to move particles and can be estimated from the equation $\omega = \rho Qs/w$ where ω is power per unit width (kg·m^{-1}·s^{-1}), Q is discharge in cubic metres per second, s is slope in percent, width (w) is in metres, and ρ is the density of water (Leopold et al. 1964). This is the work rate of flowing water per unit width of stream.

To investigate food quality a large sample of drifting organic detritus was collected from each site, divided into the eight size-classes, and the invertebrates removed. A portion of each size-class was used for chlorophyll *a*, respiration, and carbon to nitrogen (C:N) ratio estimates. Chlorophyll *a* per milligram of AFDW, corrected for phaeophyton, was estimated by extraction in 10 mL of 90% acetone for 24 h (Strickland and Parsons 1972) and the use of a Beckman spectrophotometer. After chlorophyll extraction, detritus was weighed and ashed at 550°C. Respiration was determined at our streamside laboratory with a Gilson respirometer at ambient stream temperatures (Gilson 1963). Four to six respiration estimates were made for each size-class where enough material could be collected. Samples were then ashed and weighed. C:N was determined with a Carlo Erba Elemental Analyser. Samples were dried and divided into two portions; one was used for C:N analysis and the other ashed.

Results and Discussion

CONCENTRATIONS

On an annual basis Devils Club Creek exports the highest concentration of particulate organic detritus of the four streams; the McKenzie River transports the next highest level (Table 3). Mack Creek and Lookout Creek have the lowest concentrations. The three Andrews Forest sites have similar seasonal patterns; highest concentrations are in winter and lowest concentrations during autumn when flow is minimal. The McKenzie River transports the highest concentration during spring snowmelt and lowest in early autumn.

Variations within a day are small compared to the mean transport concentration; coefficients of variation (CV) range from only 0.2% in Devils Club Creek to 29.3% in Lookout Creek (Table 3). CVs are least in spring and summer and greatest during autumn and winter. Diel variations in organic matter concentration are, however, neither regular nor of sufficient magnitude to be considered periodic.

Concentrations of organic matter transported by unaltered coniferous forest streams are usually low when compared to other streams (Sedell et al. 1979). Among

TABLE 4. DOC:POC by site and season. Mean seasonal concentration of drifting POM is assumed to be 50% carbon.

Season	Devils Club Creek	Mack Creek	Lookout Creek	McKenzie River
Winter	1.76	2.59	2.60	1.61
Spring	4.43	8.57	3.73	1.38
Summer	3.14	4.43	2.46	1.37
Autumn	4.53	6.47	7.63	2.70

TABLE 5. Average unit stream power ($\bar{x}$) calculated for each sampling date by site and season. Standard deviations are all ≤ 0.01.

Season	Devils Club Creek	Mack Creek	Lookout Creek	McKenzie River
Winter	0.07	0.17	0.12	0.56
Spring	0.40	1.14	1.26	1.46
Summer	0.07	0.27	0.15	0.84
Autumn	0.03	0.12	0.09	0.68

the more important factors contributing to the low levels are the following: efficient retention and processing by the forest and its streams, inputs of large CPOM not easily moved by currents, low nutrient concentrations limiting the development of a large biomass of primary producers, and fast currents or high precipitation eroding the stream bed to cobble or bedrock. These and other influences interact to produce the remarkably clear waters typical of western Oregon and other areas with unaltered coniferous forest streams. Where some of these factors are not as pronounced, considerable amounts of fine detritus and primary producers can accrue, contributing to higher transport concentrations.

DOC:POC Ratio

Dissolved organic carbon (DOC: $<0.45\ \mu$m) concentrations, as measured by persulfate oxidation (S. V. Gregory unpublished data), are usually less than an order of magnitude larger than the mean seasonal POC ($>0.45\ \mu$m) concentrations (Table 4). In all cases the DOC:POC ratios range from 1 to 9, being lowest in the McKenzie River and during winter for all sites.

According to Wetzel and Rich (1973), the DOC:POC ratio normally ranges from 6 to 10 in lakes and rivers, with lower ratios reported mostly from highly productive lake waters. Malcolm and Durum (1976) have reported DOC:POC ratios ranging from approximately 1 to 18 for a variety of rivers. Ratios for our sites fall into this latter range.

Stream Power

The amount of organic material transported by stream is partly a function of stream power. Unit stream power is a measure of a streams' ability to do this work. Unit stream power is generally lowest in Devils Club Creek, highest in the McKenzie River, and intermediate, and of nearly equal magnitude, in Mack Creek and Lookout Creek (Table 5). At each site, among the days sampled each season, there is little change in unit stream power. However, due to seasonal differences in discharge there is a considerable difference in unit stream power among seasons, with highest values in spring and lowest in autumn.

We are unable, however, to show a significant relationship between POM concentrations and unit stream power ($r = -0.03$, $P = 0.75$, $n = 114$), or between mean seasonal concentrations and unit stream power ($r = -0.41$, $P = 0.06$, $n = 16$) (Fig. 2). POM concentrations do not significantly respond to changes in stream power alone; however, closer examination suggests that concentration decreases with increasing unit stream power with the Andrews Forest (i.e. excluding the McKenzie River site).

Unit stream power, by itself, is not a good predictor of POM concentrations transported within a watershed, although Sedell et al. (1979) found it to be a fairly useful tool for comparisons between streams with different watershed characteristics. Organic matter concentrations within a biome watershed tend to remain within an order of magnitude. There are several factors determining that magnitude: types and amounts of organic inputs, stream power, number and type of retention structures, and frequency of flood recurrences. The flood recurrence interval for all sites is 1.2 yr. As yet, however, we have been unable to quantify all physical, chemical, and biological retention structures in these streams and determine their relation to the amount of particulate organic matter being transported. Stream power moves materials downstream while retention structures resist this movement. The interaction between these factors is of considerable importance in determining both the amount and size distribution of organic material being transported. Other factors not investigated in this study, such as the interval between

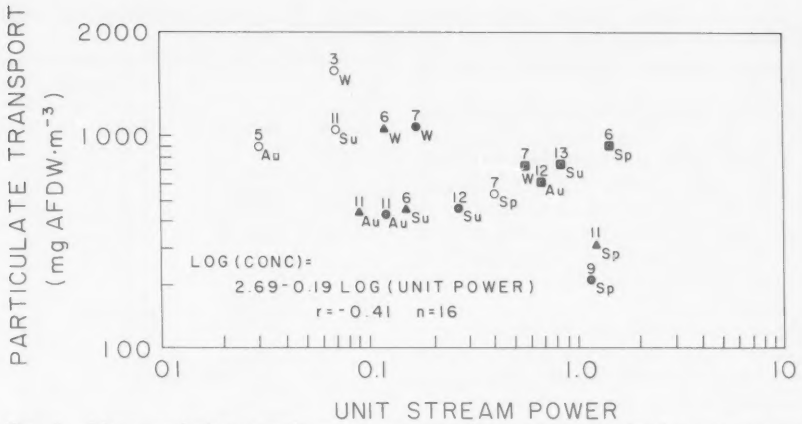

FIG. 2. Mean particulate organic matter concentrations and sample size for a season are shown as a function of unit stream power. Coefficient of variation for each power data point is <5%. ○, Devils Club Creek; ●, Mack Creek; ▲, Lookout Creek; ■, McKenzie River; W, Winter; Sp, Spring; Su, Summer; and Au, Autumn.

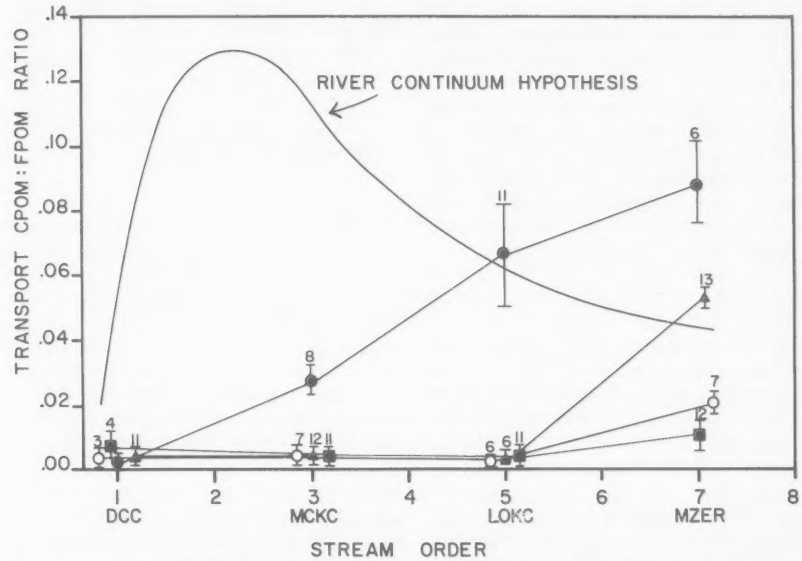

FIG. 3. CPOM:FPOM ($\bar{x} \pm$ SE, n) is shown as a function of stream order for each site and season. CPOM:FPOM values on the y-axis do not necessarily correspond to the conceptual hypothesis shown. ○, Winter; ●, Spring; ▲, Summer; ■, Autumn.

storms or whether samples are taken on a rising, falling, or stable hydrograph, will also greatly affect organic matter concentrations (Bilby and Likens 1979).

CPOM:FPOM

Vannote's River Continuum concept predicts CPOM:FPOM will decrease as stream order increases beyond the very small headwater streams that are normally without enough power to move large particles (Cummins 1975, 1977). The rationale is that small, heavily shaded forest streams receive more inputs of large organic particles in the form of wood and leaves, while large particle inputs are less important, and small organic particles relatively more important, in higher order streams. Our data are sufficient to test this concept both among stream orders and seasons. We found the concept not to be true for these four streams (Fig. 3). In spring, however, CPOM:FPOM increases with stream order, the correlation being highly significant

($r = 0.99$; $P < 0.01$). In winter, summer, and autumn, however, CPOM:FPOM approaches zero for the Andrews Forest sites, remaining only slightly higher for the McKenzie River.

Between sites the average CPOM:FPOM increases with stream order. Although there is not a statistical difference, Devils Club Creek is always the lowest and the McKenzie River highest. This probably indicates that low order streams are efficient in retaining and processing organic inputs, whereas larger order streams are not quite as effective in retaining larger particles. This can be explained, in part, by stream power and retention characteristics.

CPOM:FPOM is dependent upon the physical size of biological inputs, stream power available to move organic material and the ability of retention structures to slow downstream movements of those inputs. Vannote (in Cummins 1975, 1977) takes into account the physical size of organic inputs but does not consider power or retention structures. Although Devils Club Creek and Mack Creek have inputs of predominantly woody debris and leaves, they also have efficient retention structures to retain coarse inputs against stream power and process them in place. Should the retention structures be altered or removed, as during some logging operations, a shift in CPOM:FPOM should be readily apparent with large amounts of coarse materials being moved downstream. This happened in an experimentally clearcut watershed in the Andrews Forest (Sedell unpublished data). Little downstream transport of organic material occurred when the old-growth forest was intact but after the watershed was logged, and normal stream debris increased, huge amounts of CPOM were exported. The increase in stream debris should not be equated with an increase in permanent retention structures which would slow CPOM movement. The McKenzie River normally exports relatively large amounts of CPOM, derived mostly from vegetation along its own stream margins rather than upstream tributaries, as a result of a few retention structures and high stream power. CPOM has few places to become lodged and hence tends to readily drift.

If transport of organic detritus is to be predictable, biological inputs, stream power, retention structures, and discharge patterns must be considered as interacting variables. Stream order by itself is not a good indicator of CPOM:FPOM, since all streams export mostly small-sized particles and many larger sized particles when retention structures are absent or altered.

Percentage Composition

As reported in Sedell et al. (1979) size fractions plotted as a cumulative percentage by weight reveal an interesting feature (Fig. 4). For all sites, in all seasons, the mean particle size of organic detritus in transport is between 3 and 12 μm. Larger particles (>106 μm) may be a visually conspicuous component of the drift at times; nevertheless, the majority of the organic drift is always less than about 12 μm.

TABLE 6. Percentage composition, by weight, of drifting particulate organic matter.

Location	Season	Percentage of total transport		
		>106 μm	53–106 μm	0.45–53 μm
Devils Club Creek	Winter	5.3	8.5	86.2
	Spring[a]	1.2	—	98.8
	Summer	5.0	20.4	74.2
	Autumn	9.9	19.1	71.0
	Mean	5.45	16.0	82.6
Mack Creek	Winter	4.2	11.8	84.0
	Spring[a]	16.8	—	83.2
	Summer	9.1	16.1	74.8
	Autumn	4.2	6.0	89.8
	Mean	8.6	11.3	83.0
Lookout Creek	Winter	1.2	0.6	98.2
	Spring[a]	13.8	—	86.3
	Summer	4.7	6.1	89.3
	Autumn	1.3	9.7	89.1
	Mean	5.3	5.5	90.7
McKenzie River	Winter	8.0	7.5	84.6
	Spring[a]	18.2	5.7	76.2
	Summer	12.4	8.6	79.0
	Autumn	2.8	7.0	90.2
	Mean	10.4	7.2	82.5

[a]53–106 μm not sampled.

During normal flow Devils Club Creek exports little organic matter >106 μm (Table 6); on an annual basis it accounts for only 5% of the drift. During spring Mack Creek and Lookout Creek export 17 and 14%, respectively, of total transport in the >106-μm fraction. At other times this fraction makes up <5% of the total. During spring and summer, particle sizes >106 μm make up 13 and 12% of the total in the McKenzie River but, surprisingly, are insignificant in autumn during leaf fall. For all sites, and all seasons, more than 70% of organic particulate drift is VPOM (0.45–53 μm) (Table 6).

The fact that low order streams export >70% of particulate organic matter as VPOM suggests the possible high efficiency of small stream systems in retaining and processing organic inputs. Unaltered small streams appear to have efficient retention structures to trap inputs, allowing them to be processed. Higher order streams transport mostly VPOM since a major biological input is VPOM from upstream areas and FPOM from local periphyton and macrophytes.

It is interesting, nonetheless, that each site and season has the same mean particle size in transport and that size is always small (3–12 μm). Recent studies

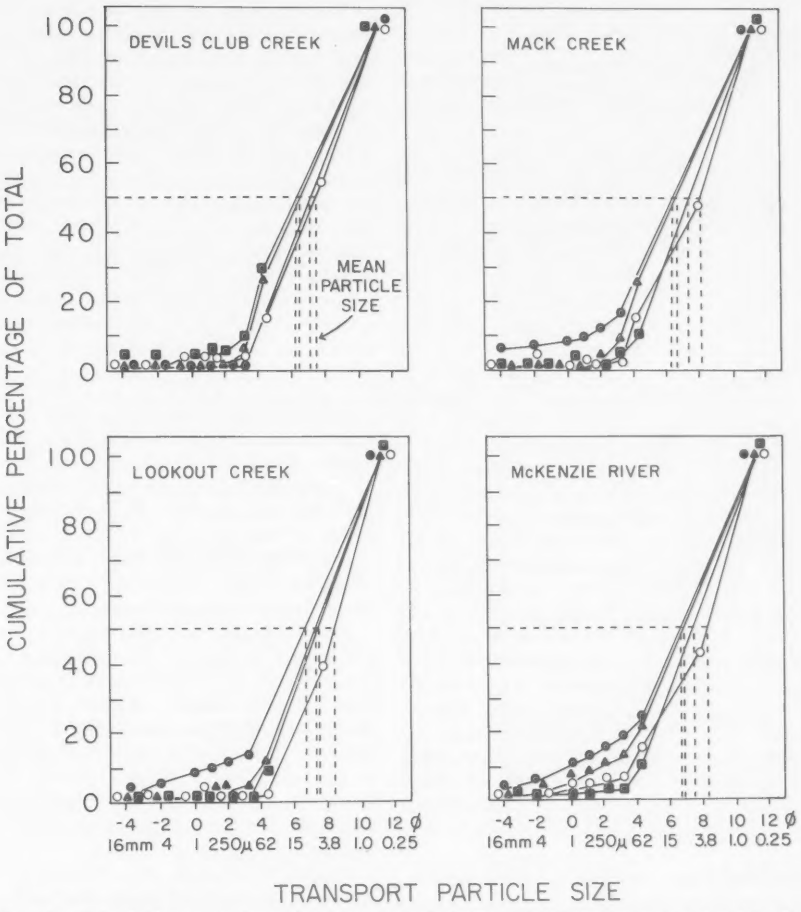

FIG. 4. Cumulative percentage of total organic drift (by weight) is shown as a function of particle size (both mm and ϕ [phi] units) for the sampling locations each season. Mean transport particle size is determined directly from the graph. $\phi = -\log_2$ (particle size, mm).

indicate many streams and rivers in a variety of watersheds transport most organic matter in the 3–20-μm size range. Seki et al. (1969) found the mean particle size for drifting organic matter in the Nanaimo River, British Columbia, to be 4 μm in summer and 20 μm in winter. Naiman (unpublished data) found the mean size range for 10 stations and all major tributaries of the Amazon River between Manaus, Brazil, and Iquitos, Peru, during the onset of flooding to be 3–15 μm.

This, however, does not explain why small particles are so abundant. In reality there seem to be only two possibilities (or a combination of both) to explain this observation. First, VPOM may be abundant because no organisms utilize it, or second, VPOM may be generated rapidly and continuously. It is a size range that can be generated from the processing of CPOM and FPOM, as well as from flocculation of DOM.

Not surprisingly there are invertebrate species adapted for feeding on drifting detritus particles in the VPOM size range (Wallace et al. 1977). Some Trichoptera have nets with mesh sizes to trap particles from 1 to 40 μm diam. Particles of this size range have been found in their guts, guts of many other Trichoptera species with larger mesh nets, and *Corbicula* clams (Wallace et al. 1977). Maciolek and Tunzi (1968) estimated that 60% of the cellular microalgae from a small California lake was removed within 0.4 km after entering a stream by filter feeding Simuliidae. These studies indicate the importance of VPOM to downstream communities and that particle sizes are selectively utilized; therefore, VPOM must be generated continuously and probably fairly rapidly.

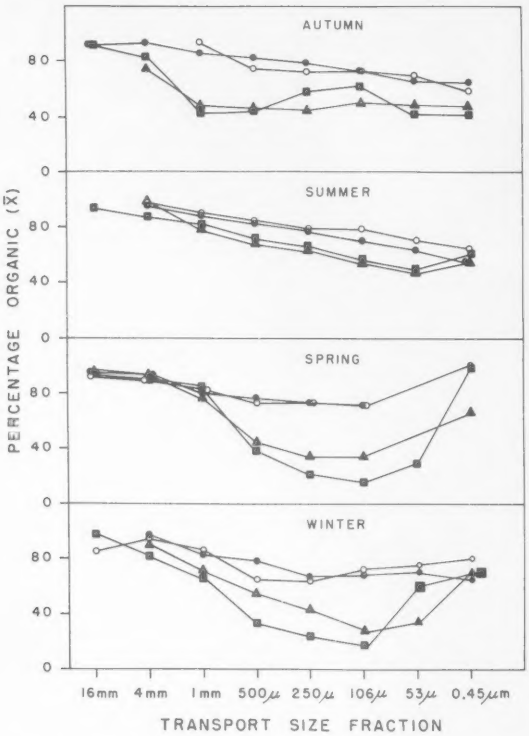

FIG. 5. Percentage organic matter is shown as a function of particle size by season for Devils Club Creek (○), Mack Creek (●), Lookout Creek (▲), and the McKenzie River (■).

FOOD QUALITY STUDIES

Food quality is defined as growth producing nutritive content per unit of food intake, whereas food quantity is defined as density per unit of environment (Cummins 1974; Ward and Cummins 1978). Food quantity and quality are obviously important in determining the distribution and abundance of invertebrate consumers and may be important in determining processing efficiencies. However, no criteria have been established for determining the quality of drifting organic matter. As a first analysis we examined percentage organic, chlorophyll *a*, C:N, and respiration rates associated with particles from the various size-groups.

Percentage organic — There are distinct differences in the percentage of organic matter among size-classes both between seasons and sites (Fig. 5). In general, percentage organic matter decreases as particle size decreases but may increase again in the 0.45-μm size-class. For sizes >1 mm the percentage of organic matter is normally >80% but decreases, depending on season and site, as particle size decreases.

The sharpest decrease in organic content with decreasing particle size is during spring and winter; summer has the slowest decline (Fig. 5). Rate of decline can also be grouped by site. Lookout Creek and the McKenzie River have the same general pattern for all seasons with a low organic content in the middle size-classes (53 μm–1 mm), while Devils Club Creek and Mack Creek show similarity in having relatively high percentage organic for all size-classes. Thus, small particle sizes are richer in organic material in low order streams than corresponding sizes in higher order streams. This could have a significant effect upon invertebrate communities in that search time for organic particles and clogging of feeding apparatus would be minimized in an environment with sufficient organic particles and few inorganic particles.

Chlorophyll — The percentage of total drifting organic material as chlorophyll *a* is estimated only for winter, summer, and autumn (Fig. 6). Organic matter concentrations are converted to carbon using empirical data and assuming a carbon:chlorophyll *a* conversion factor of 120 (Gregory 1978). Chlorophyll associated with VPOM is mostly from diatoms and microalgae while, in larger size-classes (>106 μm), it is mostly derived from leaves and needles.

There are distinct differences in the percentage of transport occurring as chlorophyll by size-class and by site, but only slight differences by season. As would be expected, the heavily shaded, lower order streams (Devils Club Creek and Mack Creek) export essentially no chlorophyll as diatoms or microalgae (Fig. 6). In Lookout Creek and the McKenzie River periphyton is abundant and contributes a relatively large percentage of the total organic matter transported (up to 92% in the McKenzie River).

Chlorophyll associated with leaves and needles is important in the McKenzie River and Lookout Creek, but of minor importance in Mack Creek. With the exception of a single input of huckleberry leaves, it is also of minor importance in Devils Club Creek. The middle size-classes (106 μm–1 mm) usually contain little chlorophyll since material in this size range is derived from decomposition of wood, leaves, needles, and mosses with nearly all chlorophyll degraded during the decomposition process.

In Lookout Creek and the McKenzie River greatest chlorophyll export is in autumn; periphyton has reached maximum biomass over the summer, is beginning to slough and, concurrently, autumn leaf fall is in process. Devils Club Creek and Mack Creek transport such small quantities of chlorophyll that seasonal differences are not apparent.

Respiration — Respiration was measured for as many particle sizes as possible in winter, summer, and autumn (Fig. 7). Water temperatures within sites are often different between seasons, but we could not demonstrate a significant relationship ($P > 0.05$) between stream

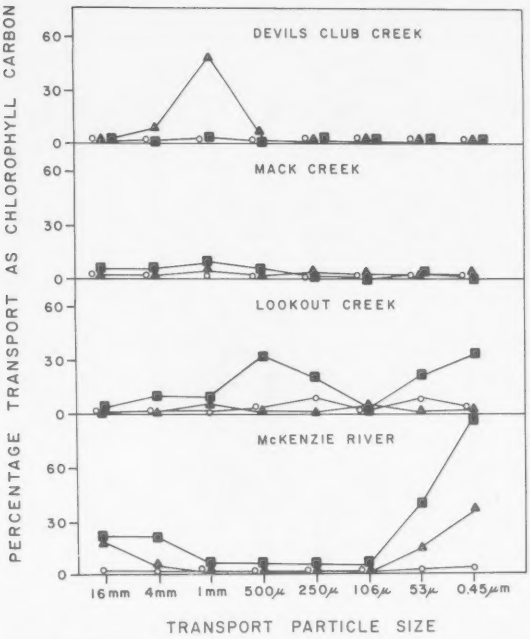

FIG. 6. Percentage of total organic transport as chlorophyll *a* derived from viable mosses and microalgae are shown for Winter (○), Summer (▲), and Autumn (■). Chlorophyll *a* associated with particles $<106\ \mu m$ is mostly derived from periphyton, while leaves and mosses contribute chlorophyll to particles >1 mm.

temperature and oxygen consumption. Also, there is no significant difference in respiration rates between seasons but there is a significant difference (ANOVA, $P < 0.05$) among sites. Respiration rates in Lookout Creek and the McKenzie River are nearly an order of magnitude higher than in the two smaller streams.

Particle size and respiration rate are positively correlated ($P < 0.01$) only in Mack Creek and the McKenzie River (Fig. 7). In general, respiration rate by particle size does not show a consistent pattern for all streams but, rather, reflects biological conditioning associated with each unique stream segment and changes occurring in the composition and origin of organic matter as it is transported downstream.

A significant correlation between respiration rate and sample weight for Mack Creek, and the nonsignificant relationship between particle size and respiration in Devils Club Creek and Lookout Creek, cast some doubt about application of the data. We believe the data are, nonetheless, sufficiently valid to approximate the magnitude of respiration by drifting particles. Total respiration by particles $>106\ \mu m$, 53–106 μm, and 0.45–53 μm has been estimated using particle size: respiration rate regressions and empirical data on organic matter concentrations (Table 7). In summer, total respiration by drifting POM ranges from 24 to 144 $\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$, while autumn estimates range from 11 to 44 $\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$. Highest rates occur, however, during winter when organic detritus concentrations are greatest (36–233 $\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$).

In most cases respiration rate decreases as particle size decreases but most oxygen consumption occurs in the 0.45–53-μm size fraction, accounting for 57–97% of total respiration (Table 7). This is a reflection of VPOM dominance of drifting POM. Particles $>106\ \mu m$ account for only 1.5–27% of the total respiration; a reflection of their relative paucity. This may present a strategy delemma to consumer species feeding on microbes. Larger particles with higher respiration rates are relatively rare, whereas smaller particles are more abundant but generally have fewer microbes per unit weight.

C:N — Devils Club Creek and, in general, Mack Creek export organic matter with higher C:N ratios than Lookout Creek or the McKenzie River (Table 8). C:N did not decrease below 17 for any particle size in Devils Club Creek while, for Mack Creek, it did so for only a few particle sizes in summer and for one size in autumn. In contrast, Lookout Creek and the McKenzie River transport particles during all seasons with C:N at, or below, 17 for most sizes <1 mm.

These results are somewhat deceiving since, for many of the low C:N ratios, the percentage carbon in the samples is also small (Table 8). Carbon percentages for most samples are at least 30% but may decline below this level for small particle sizes in Lookout Creek and McKenzie River; indicating low C:N ratios may partially result from defractile nitrogen normally unavailable to microbes or consumers.

Food quality — Organic material drifting downstream represents a one-way coupling of energy from upstream areas to downstream reaches (Webster 1975). Webster (1975) and Wallace et al. (1977) discuss the concept of "spiralling" where the greater the amount of material cycling within a stream, the more efficient the stream is in processing organic matter and nutrients. Spiralling may be envisioned as a process whereby material is retained, then released, retained again, released, etc. When little spiralling occurs the system is inefficient and much material is moved downstream without being utilized. Wallace et al. (1977) reviewed the role of filter feeders in this process but did not give detailed analysis of food quality that might affect invertebrate distribution and abundance and thus the efficiency of streams in retaining and processing organic matter. Food quality is obviously important in determining the degree of spiralling and, in turn, the effectiveness of the system in retaining and processing organic material.

Microalgae are considered to be good quality foods because of their protein and lipid content but small heavily shaded streams have poorly developed

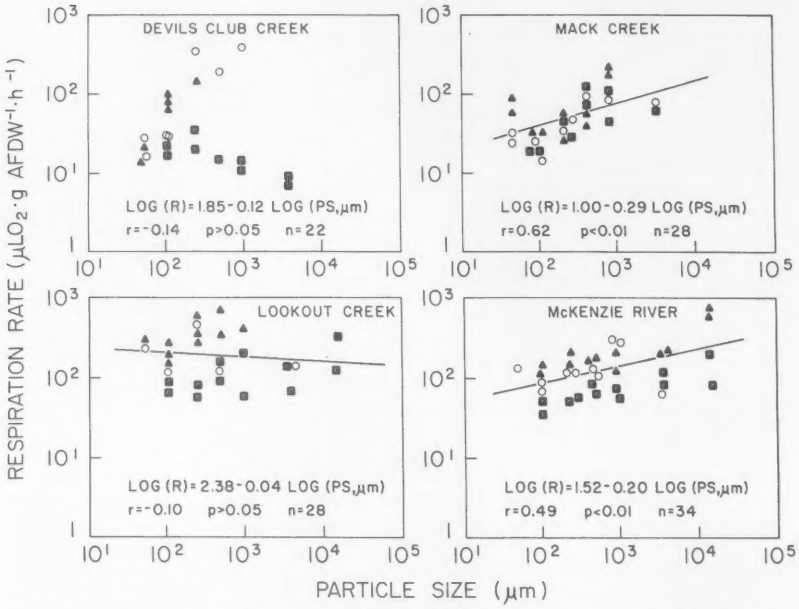

FIG. 7. Respiration is shown as a function of particle size for each stream: Winter (○), Spring (●), Summer (▲), Autumn (■).

TABLE 7. Total respiration of drifting particulate organic matter by particle size, site, and season.

Season	Particle size	Devils Club Creek		Mack Creek		Lookout Creek		McKenzie River	
		$\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$	%	$\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$	%	$\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$	%	$\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$	%
Winter	>106 μm	10.6	29.9	2.0	5.4	5.3	2.3	7.2	8.0
	53–106 μm	2.6	7.3	4.3	11.7	1.5	0.6	6.8	7.5
	0.45–53 μm	22.3	62.8	30.4	82.9	225.8	97.1	76.0	84.4
	Total	35.5	100.0	36.7	100.0	232.6	100.0	89.0	99.9
Summer	>106 μm	4.0	16.5	2.0	5.6	6.9	4.8	16.5	18.8
	53–106 μm	4.5	18.3	6.0	16.7	8.8	6.1	7.0	8.0
	0.45–53 μm	15.9	65.2	28.2	77.8	128.7	89.1	64.1	73.2
	Total	24.4	100.0	36.2	100.1	144.4	100.0	87.6	100.0
Autumn	>106 μm	1.6	8.3	0.7	6.3	0.6	1.5	1.7	5.8
	53–106 μm	3.7	19.4	0.6	5.9	4.3	9.6	1.9	6.8
	0.45–53 μm	13.9	72.3	9.6	87.8	39.2	88.9	24.8	87.4
	Total	19.2	100.0	10.9	100.0	44.1	100.0	28.3	100.0

periphyton communities. In larger streams the canopy is open and the periphyton community well developed. During the normal course of growth and decay, periphyton sloughs a considerable amount of material to downstream reaches (Swanson and Backmann 1976; Liaw and MacCrimmon 1977; Naiman and Sibert 1978). In Lookout Creek and McKenzie River, during summer and autumn, chlorophyll accounts for a significant percentage of total drift (Fig. 6). Since only chlorophyll *a* was measured, detritus produced from decomposing periphyton was not detected. In autumn, however, as the periphyton community is waning, microalgae may be a considerable proportion of material transported in larger streams and, thus, may contribute to lower C:N ratios in downstream reaches.

Russell-Hunter (1970) indicated that a C:N of about 17 or less is necessary for efficient feeding and growth in most aquatic organisms. However, Ward and Cummins (1978) found the nitrogen content of detritus to be the least useful of the several parameters tested as growth-predictors for the collector *Paratendipes albimanus* (Chironomidae). They concluded that, de-

TABLE 8. C:N and percentage carbon of drifting particulate organic matter by size-group and season for each sampling location.

Season	Particle size	Devils Club Creek		Mack Creek		Lookout Creek		McKenzie River	
		%C	C:N	%C	C:N	%C	C:N	%C	C:N
Winter	16 mm	—[a]	—[a]	—[a]	—[a]	—[a]	—[a]	32.8	18.5
	4 mm	—[a]	—[a]	—[a]	—[a]	43.8	15.8	43.3	19.9
	1 mm	—[a]	—[a]	45.6	25.3	17.9	17.4	33.7	13.0
	500 μm	34.6	32.9	44.3	28.5	16.7	12.7	36.7	14.4
	250 μm	35.4	36.1	41.7	27.8	17.0	12.6	37.7	15.2
	106 μm	36.1	34.0	36.8	33.1	17.2	12.5	38.3	19.0
	53 μm	36.2	35.8	30.4	24.9	—[a]	—[a]	36.7	20.6
Spring	16 mm	49.4	80.9	51.5	24.3	—[a]	—[a]	43.1	23.7
	4 mm	46.8	30.6	48.1	23.9	43.0	18.1	50.2	23.5
	1 mm	45.2	27.9	47.7	26.9	45.6	15.1	47.3	13.8
	500 μm	40.7	22.2	45.6	23.5	—[a]	—[a]	10.9	11.4
	250 μm	39.5	26.0	37.7	20.7	14.0	8.5	9.5	15.1
	106 μm	40.5	31.4	27.8	20.7	22.5	19.9	7.3	17.0
Summer	16 mm	—[a]	—[a]	—[a]	—[a]	—[a]	—[a]	49.4	38.0
	4 mm	—[a]	—[a]	—[a]	—[a]	46.0	17.4	52.5	14.2
	1 mm	—[a]	—[a]	46.1	19.4	39.5	8.3	46.6	15.2
	500 μm	—[a]	—[a]	45.5	15.4	33.3	9.7	36.8	14.3
	250 μm	41.7	34.9	41.3	20.7	31.7	10.5	34.5	14.5
	106 μm	41.8	22.5	36.4	18.0	30.2	9.6	28.6	17.3
	53 μm	36.5	19.9	32.0	14.8	19.3	10.7	15.7	12.1
Autumn	16 mm	—[a]	—[a]	48.8	31.9	—[a]	—[a]	47.5	22.0
	4 mm	—[a]	—[a]	51.0	37.2	51.5	30.6	45.9	22.7
	1 mm	—[a]	—[a]	51.3	36.7	23.6	21.5	10.8	15.2
	500 μm	—[a]	—[a]	46.6	30.1	5.4	12.3	4.0	15.0
	250 μm	40.0	28.8	5.9	9.9	11.9	14.2	40.4	37.8
	106 μm	41.6	28.9	8.9	19.4	16.6	17.1	37.1	30.4

[a]Either not enough material collected for analysis or the sample was lost.

spite a low C:N ratio, much of the nitrogen in downstream drift is of a refractory nature and not readily utilized by the associated microbes which constitute the primary nutritive source for the midge. With this in mind the importance of our C:N data must be interpreted with caution. To some extent the data support Ward and Cummins (1978) in that C:N is lower in Lookout Creek and the McKenzie River than in Devils Club Creek or Mack Creek, and some may be refractory nitrogen from areas far upstream. Also, the consumer invertebrate community is best developed in Mack Creek (Hawkins, Naiman, and Sedell unpublished data).

Nearly all drifting POM in Devils Club Creek and Mack Creek is derived from woody debris and leaves with inherently high C:N ratios. However, it is not known how much VPOM is of direct terrestrial input and, therefore, subjected to preprocessing in the terrestrial system. Wood and leaves sufficiently conditioned have low C:N ratios, and probably represent most material >106 μm. The low C:N ratio in material <106 μm partially results from periphyton, but could also be due to low amounts of carbon or high levels of refractory nitrogen. In any case, much of the material being transported in larger streams has the potential to be a good food source if the Russell-Hunter (1970) proposed C:N $\leq$ 17 range is correct.

Ward and Cummins (1978) found a good correlation between invertebrate growth and detritus respiration and ATP, respiration being used as an index of microbial activity on particles and ATP as an estimate of microbial biomass. Respiration rates on drifting organic particles are the same magnitude as organic particles in the substrate (Naiman and Sedell unpublished data), but do not correspond to the general relationships found by Hargrave (1972) for benthic detritus. In our measurements particle size and respiration rates are either positively correlated or there is no correlation (Fig. 7); for sediments an inverse relationship has been found (Hargrave 1972; Odum and de la Cruz 1967; Fenchel 1970). Hargrave (1972) related this negative relationship for sediments to surface area available for microbial colonization. This logical conclusion, however, does not hold for drifting organic particles. Bacteria on transported particles may produce growth regulating substances (Burkholder 1963), detritus may become more and more refractory as particles are decomposed and reduced in size, or bacteria could be physically removed by turbulence. The low respiration rates would support any of these

postulates. Hargrave (1972) found rates for a wide variety of sediments to range from 0.1 to 10 mg $O_2 \cdot g$ $AFDW^{-1} \cdot h^{-1}$. In our experiments most rates ranged from 0.03 to 0.52 mg $O_2 \cdot g$ $AFDW^{-1} \cdot h^{-1}$; clearly at the low extreme. Whatever the cause, bacterial respiration on drifting organic matter is not great but, perhaps, the Gilson respirometer is not a good simulator for drifting particles. However, given the fact that respiration rates are higher on corresponding particle sizes in Lookout Creek and the McKenzie River than in the lower order streams, it can be concluded that drifting particles have a greater microbial activity in downstream reaches and, therefore, that the presumed food quality is better.

Acknowledgments

We thank K. Luchessa, C. Hawkins, and D. McCullough for assistance with the sampling program and M. J. Klug for analysis of samples for carbon and nitrogen. Discussions, advice, and critical readings of the manuscript by Drs. K. W. Cummins, C. E. Cushing, S. G. Fisher, J. C. Mason, G. W. Minshall, R. C. Petersen, R. L. Vannote, and numerous other colleagues greatly contributed to the completion of this project. Financial support from the National Science Foundation (BMS 75-0733) is gratefully acknowledged. This is contribution No. 5 from the River Continuum Project.

BERNTSEN, C. M., AND J. ROTHACHER. 1959. A guide to the H. J. Andrews Experimental Forest. USDA Forest Service, Pac. NW Forest and Range Exp. Sta. 21 p.

BILBY, R. E., AND G. E. LIKENS. 1979. Effect of hydrologic fluctuations on the transport of fine particulate organic carbon in a small stream. Limnol. Oceanogr. (In press)

BOLING, R. H., E. D. GOODMAN, J. A. VAN SICKLE, J. O. ZIMMER, K. W. CUMMINS, R. C. PETERSEN, AND S. R. REICE. 1975. Toward a model of detritus processing in a woodland stream. Ecology 56: 141–151.

BRINSON, M. M. 1976. Organic matter losses from four watersheds in the humid tropics. Limnol. Oceanogr. 21: 572–582.

BURKHOLDER, P. R. 1963. Some nutritional relationships among microbes of sea sediments and waters, p. 133–150. *In* C. H. Oppenheimer [ed.] Symposium on marine microbiology. Charles C. Thomas, New York, N.Y. 769 p.

CHANDLER, D. C. 1937. Fate of typical lake plankton in streams. Ecol. Monogr. 7: 445–479.

CUMMINS, K. W. 1974. Structure and function of stream ecosystems. BioScience 24: 631–641.

1975. The ecology of running waters; theory and practice, p. 277–293. *In* D. B. Baker, W. B. Jackson, and B. L. Prater [ed.] Proc. Sandusky River Basin Sym.: 475 p.

1977. From headwater streams to rivers. Am. Biol. Teacher. 39: 305–312.

EGGLISHAW, H. J., AND P. E. SHACKLEY. 1971. Suspended organic matter in fast-flowing streams in Scotland. I. Downstream variations in microscopic particles. Freshwater Biol. 1: 273–285.

FENCHEL, T. 1970. Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. Limnol. Oceanogr. 15: 14–20.

FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43: 421–439.

GILSON, W. E. 1963. Differential respirometer of simplified and improved design. Science 141: 531–532.

GREGORY, S. V. 1978. Primary production in streams of the Cascade Mountains. Ph.D. Dissertation, Oregon State Univ., Corvallis, Oreg. 128 p.

HARGRAVE, B. T. 1972. Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. Limnol. Oceanogr. 17: 583–596.

HOBBIE, J. E., AND G. E. LIKENS. 1973. Output of phosphorus, dissolved organic carbon, and fine particulate carbon from Hubbard Brook watersheds. Limnol. Oceanogr. 18: 734–742.

LEOPOLD, L. B., M. G. WOLMAN, AND J. P. MILLER. 1964. Fluvial processes in geomorphology. W. H. Freeman, San Francisco. 522 p.

LIAW, W. K., AND H. R. MACCRIMMON. 1977. Assessment of particulate organic matter in river water. Int. Rev. Gesamten Hydrobiol. 62: 445–463.

MACIOLEK, J. A., AND M. G. TUNZI. 1968. Microseston dynamics in a simple Sierra Nevada lake-stream ecosystem. Ecology 49: 60–75.

MALCOLM, R. L., AND W. H. DURUM. 1976. Organic carbon and nitrogen concentrations and annual organic load of six selected rivers of the United States. U.S. Geol. Surv. Water Supply Paper 1817-F.

NAIMAN, R. J. 1976. Primary production, standing stock, and export of organic matter in a Mohave Desert thermal stream. Limnol. Oceanogr. 21: 60–73.

NAIMAN, R. J., AND J. R. SIBERT. 1978. Transport of nutrients and carbon from the Nanaimo River to its estuary. Limnol. Oceanogr. 23: 1183–1193.

ODUM, E. P., AND A. A. DE LA CRUZ. 1967. Particulate organic detritus in a Georgia salt marsh estuarine ecosystem, p. 383–388. *In* G. H. Lauff [ed.] Estuaries. Publ. Am. Assoc. Advan. Sci. 83.

RUSSELL-HUNTER, W. D. 1970. Aquatic productivity: an introduction to some basic aspects of biological oceanography and limnology. MacMillan and Company, Ltd., London. 306 p.

SEDELL, J. R., R. J. NAIMAN, K. W. CUMMINS, G. W. MINSHALL, AND R. L. VANNOTE. 1979. Transport of particulate organic material in streams as a function of physical processes. Verh. Int. Verein. Limnol. 20: (In press)

SEDELL, J. R., F. J. TRISKA, AND N. S. TRISKA. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. Verh. Int. Verein. Limnol. 19: 1617–1627.

SEKI, H., K. V. STEPHENS, AND T. R. PARSON. 1969. The contribution of allochthonous bacteria and organic materials from a small river to a semi-enclosed area. Hydrobiologia 66: 27–47.

STEPHENS, K., R. W. SHELDON, AND T. R. PARSONS. 1967. Seasonal variations in the availability of food for benthos in a coastal environment. Ecology 47: 852–855.

STRAHLER, A. N. 1957. Quantitative analysis of watershed

geomorphology. Trans. Am. Geophy. Union 38: 913–920.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis, 2nd Edition. Bull. Fish. Res. Board Can. 167: 307 p.

SWANSON, C. D., AND R. W. BACKMANN. 1976. A model of algae exports in some Iowa streams. Ecology 57: 1076–1080.

WALLACE, J. B., J. R. WEBSTER, AND W. R. WOODALL. 1977. The role of filter feeders in flowing waters. Arch. Hydrobiol. 79: 506–532.

WARD, G. M., AND K. W. CUMMINS. 1978. Effects of food quality on growth rate and life history of a stream collector (*Paratendipes albimanus* (Meigen) (Diptera:Chironomidae)). Ecology 59: (In press)

WATERS, T. F. 1969. Invertebrate drift-ecology and significance to stream fishes, p. 121–134. *In* T. G. Northcote [ed.] Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver, B.C.

WEBSTER, J. R. 1975. Analysis of potassium and calcium dynamics in stream ecosystems on three southern Appalachian watersheds of contrasting vegetation. Ph.D. Dissertation, Univ. Georgia, Athens, Ga. 232 p.

WETZEL, R. G., AND P. H. RICH. 1973. Carbon in freshwater systems, p. 241–163. *In* G. M. Woodwell and E. V. Pecan [ed.] Carbon and the Biosphere. Proc. 24th Brookhaven Symp. Biol. Nat. Technical Information Service, Springfield, Virginia. CONF-720510.

Paralytic Shellfish Toxins in the Sea Scallop, *Placopecten magellanicus*, in the Bay of Fundy

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The paralytic shellfish poison of the giant sea scallop, *Placopecten magellanicus* (Gmelin), from the Bay of Fundy has been analyzed. Of eight toxins isolated, seven were identified with those previously recognized in various sources including the Atlantic toxic dinoflagellate, *Gonyaulax tamarensis* cells. The major components were gonyautoxin-I, gonyautoxin-II, and neosaxitoxin; saxitoxin was responsible for only a very small portion of the total toxicity. A minor toxin that was eluted between neosaxitoxin and saxitoxin in the chromatography system was found to be new and designated as gonyautoxin-VII.

Key words: paralytic shellfish poisons, gonyautoxins, neosaxitoxin, *Gonyaulax tamarensis*

HSU, C. P., A. MARCHAND, Y. SHIMIZU, AND G. G. SIMS. 1979. Paralytic shellfish toxins in the sea scallop, *Placopecten magellanicus*, in the Bay of Fundy. J. Fish Res. Board Can. 36: 32–36.

Nous avons analysé le toxique responsable de la paralysie des mollusques trouvé chez le pétoncle géant, *Placopecten magellanicus* (Gmelin), de la baie de Fundy. Des huit toxines isolées, sept sont semblables à celles déjà identifiées dans diverses sources, y compris les cellules du dinoflagellé toxique de l'Atlantique, *Gonyaulax tamarensis*. Les principaux composants sont la gonyautoxine-I, la gonyautoxine-II et la néosaxitoxine; la saxitoxine n'est responsable que d'une très faible portion de la toxicité totale. Nous avons découvert une nouvelle toxine mineure éluée entre la néosaxitoxine et la saxitoxine dans le système chromatographique, et nous la désignons sous le nom de gonyautoxine-VII.

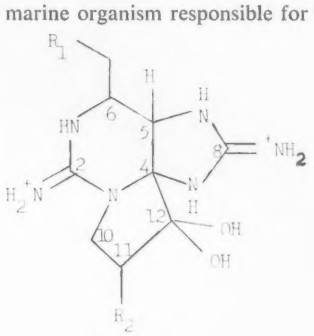
Received May 4, 1978
Accepted October 12, 1978

Reçu le 4 mai 1978
Accepté le 12 octobre 1978

Toxic shellfish are found sporadically in many parts of the world. However, some areas are troubled consistently due to frequent blooms of toxic marine dinoflagellates. The shellfish that feed upon these dinoflagellates become toxic as they collect and accumulate the toxins. Consumption of these toxic shellfish can result in a severe and often fatal form of food poisoning in humans, therefore creating a major health problem.

On the Pacific coast of North America the causative dinoflagellate of paralytic shellfish poisoning (PSP) has been identified as *Gonyaulax catenella* and the toxic shellfish along that coast include the California mussel *Mytilus californianus*, and the Alaska butter clam, *Saxidomus giganteus* (Schantz et al. 1957, 1966). The toxin isolated from these shellfish and from *G. catenella* has been identified as saxitoxin (1), a potent neurotoxin.

On the Atlantic coast, where a parallel problem exists, the marine organism responsible for PSP is *Gonyaulax*



1 R_1: $-OCNH_2$, R_2: -H Saxitoxin
2 R_1: $-OCNH_2$, R_2: α-OH Gonyautoxin-II
3 R_1: $-OCNH_2$, R_2: β-OH Gonyautoxin-III
4 R_1: -OH, R_2: -H Decarbamoylsaxitoxin

[1]All inquiries should be made to Y.S.

Printed in Canada (J5236)
Imprimé au Canada (J5236)

tamarensis.[2] The relationship between the occurrence of the causative organism and toxic shellfish has been well documented (Medcof et al. 1947; Needler 1949; Prakash 1963, 1967). The Bay of Fundy is the major geographical focal point of this problem along the Atlantic coast. Species of shellfish found to be toxic in these waters include *Mya arenaria*, *Mytilus edulis*, and *Placopecten magellanicus* (Prakash et al. 1971).

Schantz (1960) studied and attempted to isolate the toxin from toxic sea scallops, *Placopecten magellanicus* (*Pecten grandis*), which were collected during a red tide outbreak of *G. tamarensis* in the Bay of Fundy. However, he failed to isolate the toxins from these scallops even though the method he used had been successful in isolating saxitoxin from the Pacific coast shellfish. He assumed that either the chemical properties of the scallop poison were different from those of clam and mussel toxins isolated on the Pacific coast or that there were some interfering substances that prevented the toxin absorption on the weakly acidic resin. A later effort by Schantz's group with the same scallops resulted in the isolation of saxitoxin. They speculated that a conversion of less basic precursors to saxitoxin upon aging of the scallop during prolonged storage in acidic solution was responsible for the discrepancy between this result and the earlier investigation (Ghazarossian et al. 1974).

In 1975, working with the toxic soft-shell clam, *Mya arenaria*, which was collected during the severe *G. tamarensis* blooms along the New England coast in 1972 and 1974, Shimizu et al. (1975) succeeded in the isolation of a series of toxins. Later the isolation work was extended to cultured *G. tamarensis*, and a total of seven toxins, gonyautoxin-I, -II, -III, -IV, -V, neosaxitoxin, and saxitoxin were identified (Oshima et al. 1977).

Buckley et al. (1976) also reported the presence of a "major" and a "minor" toxin in the 1972 toxic soft-shell clam from the New Hampshire coast, and later it was confirmed that this "major" toxin was identical with gonyautoxin-II while the "minor" toxin was saxitoxin (Buckley and Shimizu unpublished data). The structures of gonyautoxin-II and -III (2 and 3) were studied and proposed as the 11-hydroxyl derivatives of saxitoxin (Shimizu et al. 1976).

However, the actual toxins of the deep-sea scallops have not yet been fully identified. The study of the scallop toxins is interesting because the following characteristics of scallop toxicity: (1) unlike other shellfish sea scallops retain their toxicity for longer periods of time (Medcof et al. 1947); (2) sea scallops show high toxicity in winter, which is quite different from observations with soft-shell clams and mussels (Bourne 1965); and (3) a biotransformation of toxins may occur in scallops as observed with neosaxitoxin in soft-shell clams (Shimizu et al. 1977).

The purpose of this study was to analyze the toxins involved in the toxic sea scallops and to relate the result to the above toxicity behaviors concerning the sea scallops.

Materials and Methods

Toxic Sea Scallops

Toxic sea scallops were collected in the Bay of Fundy in October 1977. The specimens were taken from a depth of 90 ± 5 m at a site approximately 10 km off Centerville, Digby Co., Nova Scotia (44°36'N, 66°05'W). The toxin concentration in selected tissues of the sea scallops was the following (as micrograms saxitoxin equivalent per 100 g sample): muscle <40; rims 4500, gonad 2400; hepatopancreas 50 000; and gills 570 (G. Jamieson, Department of Fisheries and Oceans, Biological Station, St. Andrews, N.B., personal communication). Because the edible portion of the scallop contained no detectable toxin, it was removed and the remaining viscera were collected and kept frozen at −29°C before analysis.

The viscera were thawed and drained to give 117 g of solids and 120 mL of fluids. The toxicities of these materials were assayed to be 50 000 mouse units (MU) (9000 μg saxitoxin equivalent) and 17 400 MU (3160 μg saxitoxin equivalent), respectively, by the AOAC method (AOAC 1975).

The drained viscera (82 g) were homogenized with 100 mL of acidified 95% ethanol (pH 2.3) in a Waring blender. The homogenate was centrifuged at 1500 rpm and the residue was extracted (×4) with 80% ethanol (pH 2.8). The supernatants were combined and concentrated, yielding an opaque brownish solution (50 mL). This was washed 3 times with chloroform (15 mL/washing) followed by backwashing the chloroform layers with distilled water (×3). The combined aqueous layers were concentrated in vacuo to 30 mL. The total toxicity of this extract was 33 000 MU.

Chromatography and Electrophoresis

The sample (30 mL) was chromatographed on a Bio-Gel P-2 (200–400 mesh, Bio-Rad Laboratories) column (4 × 100 cm) and eluted first with distilled water (600 mL) to remove the impurities. Fractions (15–20 mL/8 min) were collected and checked by spot test and mouse assay. No appreciable amount of toxin was found in the water eluate. The eluant was then switched to 0.03 N (mol/L) acetic acid to elute the bound toxin from the column. The fractions that gave a positive fluorescence reaction with 1% hydrogen peroxide solution (Buckley et al. 1976) were combined and concentrated to 23 mL. This concentrate had a total toxicity of 31 000 MU.

The toxin solution (23 mL) from the Bio-Gel P-2 column was lyophilized and the residue was dissolved in 2-mL glass distilled water. From this solution a 1-mL aliquot was charged on a Bio-Rex 70 (H^+ form, −400 mesh; Bio-Rad Laboratories) column (1 × 55 cm). The column was subsequently eluted with the following: (1) 0–0.03 N acetic acid linear gradient, 250 mL total; (2) 0.03–1.3 N acetic acid linear gradient, 250 mL total; and (3) 1.3 N acetic acid, 100 mL, using a constant flow pump (Milton Roy Minipump) at 3×10^3 g/cm^2. The fractions (4.5 mL each)

[2]Although the nomenclature *G. excavata* has been suggested for this toxic organism (Loeblich and Loeblich 1975), we incline to use *G. tamarensis* in this paper to keep consistency with our early reports.

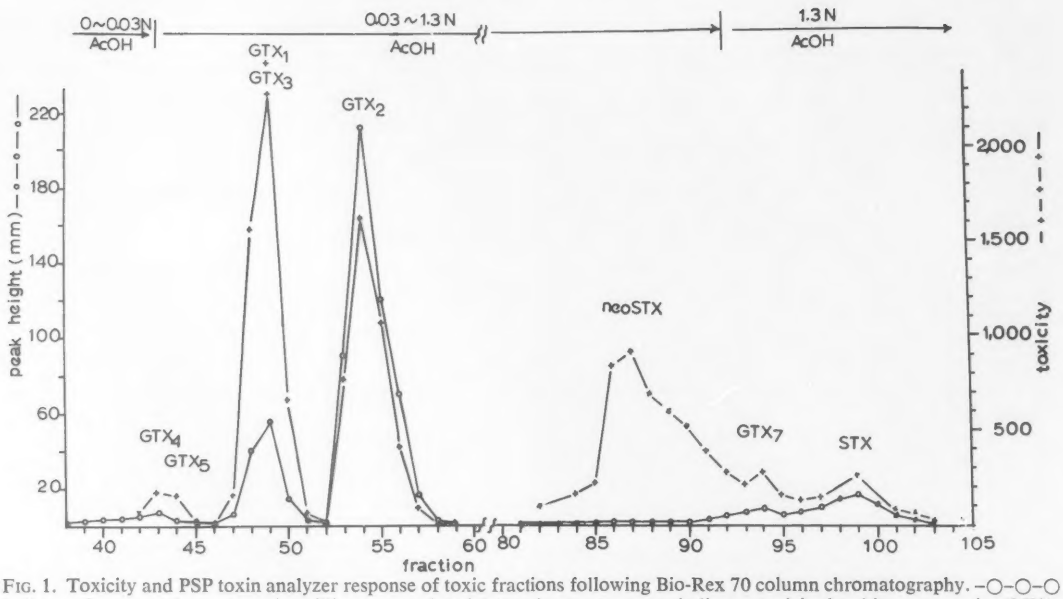


FIG. 1. Toxicity and PSP toxin analyzer response of toxic fractions following Bio-Rex 70 column chromatography. –○–○–○ indicates fluorometric response in millimetres peak height, and –+–+–+–+ indicates toxicity level in mouse units (MU). GTX_1, GTX_2, etc. are abbreviations for gonyautoxin-I, gonyautoxin-II, and so on (see Table 1 for abbreviations of all toxins). Both gonyautoxin-I (GTX_1) and neosaxitoxin (neoSTX) do not give fluorometric response but they demonstrate comparable toxicity as saxitoxin on mouse assay. Gonyautoxin-VII (GTX_7) is discovered first time in this survey and its identity needs further investigation.

were collected at 8-min intervals and checked by spot test as described above. All spot positive fractions were examined by (1) mouse assay, (2) thin-layer chromatography, and (3) fluorometry using the PSP toxin analyzer (Buckley et al. 1978).

Thin-layer chromatography (tlc) was performed on Silica Gel 60 precoated plates (E. Merck Laboratories) in pyridine, ethyl acetate, water, and acetic acid (75:25:20:15 vol/vol) for 3 h. The plates were viewed under long wave UV light (350 nm) after spraying with 1% hydrogen peroxide solution and heating.

Electrophoresis was conducted on cellulose acetate membrane strips (Schleicher and Schuel No. 2500) in an electrophoresis cabinet (Thomas Model 20) at 250 V for 1.5 h using a buffer system consisting of 0.01 M (mol/L) barbital and 0.05 M sodium barbital (pH 8.4) (Fallon and Shimizu 1977).

PREPARATION OF DECARBAMOYLSAXITOXIN (4)

Saxitoxin (10 mg) was heated in 7.5 N hydrochloric acid at 100°C for 3 h. The resulting brown solution was dried over sodium hydroxide pellets overnight. The residue was dissolved in 1 mL of distilled water and chromatographed on a Bio-Rex 70 column (-400 mesh, 1 × 50 cm) using acetic acid linear gradient from 0.1 to 1.3 N as eluant. The toxic fractions were collected, concentrated, and lyophilized to give decarbamoylsaxitoxin in 62% yield (5.4 mg).

Results and Discussion

Analysis of the toxins isolated from *Placopecten magellanicus* viscera indicated that the majority of the toxin consisted of a mixture of gonyautoxin-I, -II, -III, and neosaxitoxin (Fig. 1). These toxins accounted for 87% of the total toxicity with gonyautoxin-I and -III, gonyautoxin-II, and neosaxitoxin making up 30, 25, and 32%, respectively.[3] Gonyautoxin-IV, -V, saxitoxin, and a new toxin (tentatively named as gonyautoxin-VII)[4] made up the remainder of the toxicity. Saxitoxin, the only component previously identified in scallops from the Bay of Fundy, constituted only a very minor portion of the total toxicity (6.4%). The total profile of the toxin content in these scallops was very similar to that found in cultured *G. tamarensis* cells (Oshima et al. 1977) except for the higher concentration of gonyautoxin-I in the sea scallops. Furthermore, in comparison with the *G. tamarensis* contaminated soft-shell clams, *Mya arenaria*, the scallops contained high concentration of neosaxitoxin, whereas in *M. arenaria* only a trace amount of neosaxitoxin was discovered. Although the structure elucidation of neosaxitoxin is still in progress, in vitro studies clearly show that neosaxitoxin is easily

[3]Gonyautoxins (I–IV) and neosaxitoxin have the specific toxicity comparable to that of saxitoxin, 5000 mouse units/mg ± 500 (unpublished data). Also, because gonyautoxin-I and neosaxitoxin failed to give response to the fluorometric measurement (Buckley et al. 1978), the percentage of each toxin can be calculated from Fig. 1.

[4]An unknown toxin isolated from European mussels contaminated with a *Gonyaulax* sp. was designated as gonyautoxin-VI (Hsu et al. unpublished data).

TABLE 1. Chromatographic and electrophoretic behavior of paralytic shellfish poisons in the sea scallops, *Placopecten magellanicus*.

Toxin	Elution order from Bio-Rex 70 Column	tlc[b] Rf	Relative electrophoretic mobility
gonyautoxin-V (GTX_5)	1	0.47	0.46
gonyautoxin-IV (GTX_4)	2	0.74	0.34
gonyautoxin-I (GTX_1)	3	0.80	0.46
gonyautoxin-III (GTX_3)	4	0.61	0.60
gonyautoxin-II (GTX_2)	5	0.70	0.72
neosaxitoxin (neoSTX)	6	0.65	0.60
gonyautoxin-VII (GTX_7)	7	0.46	0.97
saxitoxin (STX)	8	0.53	1.00
decarbamoylsaxitoxin[a]	—	0.43	1.10

[a]Synthetic decarbamoylsaxitoxin is listed for comparison.
[b]Thin-layer chromatographic (tlc) condition given in the text.

converted to saxitoxin through reduction (Shimizu et al. 1977), and we speculate that a possible biochemical conversion of neosaxitoxin to saxitoxin may also occur in *M. arenaria*. This would account for the minimal amounts of neosaxitoxin found in this clam. If we can assume that the causative organism in the Bay of Fundy produces the same toxins as our cultured *G. tamarensis*, the large concentration of neosaxitoxin found in the sea scallop suggests the lack of biochemical facilities in the sea scallop to reduce neosaxitoxin to saxitoxin.

The scallop's ability to retain the toxicity for a length of time, even in the winter, has been a puzzle in the past. This is especially true in view of the fact that the shellfish live in a depth where the presence of a large population of motile dinoflagellates is questionable. In our study the motile dinoflagellates release toxins immediately upon their death, which excludes the chance for scallops to acquire the toxin from the dead bodies of dinoflagellates. Regarding the sources of toxins in the scallops, one can envisage such possibilities as the uptake of cysts, secondary food chain, or symbiosis. Alaska butter clams are also known to retain the toxicity year-round. However, our studies in the past indicated that these clams have a toxin profile totally different from other toxic shellfish specimens including mussels collected from the proximate areas (Oshima et al. 1977; Shimizu et al. 1978). Presumably the Alaska butter clams accumulate toxins by a mechanism that is more complicated than simple ingestion of causative organisms. The presented analytical results of scallops did not show such a drastic difference as in Alaska butter clams. The major toxins found in the scallop also exist as the predominant components in *G. tamarensis* and the other shellfish that ingested the organism. This may indicate that the out-of-phase unusually high toxicity of this deep-sea scallop comes simply by the uptake of cyst forms as suggested previously (Bourne 1965). If that is the case, there seems to be no large difference between the toxin components of the motile and cyst form of *G. tamarensis*. However, it is not clear at this stage whether the slight differences in the relative concentrations and the presence of a new minor toxin, gonyautoxin-VII, in the scallop reflect the toxin contents in the cyst form or biotransformation in the scallop. For an unequivocal conclusion, it is necessary to carry out the exact analysis of toxins in the cyst form. At present, the work on cyst form of *G. tamarensis* is underway in our laboratory.

The new toxin (gonyautoxin-VII) discovered in the sea scallops showed a very close ascending mobility on tlc (Table 1) as decarbamoylsaxitoxin (4) (Ghazarossian et al. 1976). The elution pattern of gonyautoxin-VII from the Bio-Rex 70 column also resembled that of decarbamoylsaxitoxin. However, comparison on electrophoresis indicated that the two compounds are not actually identical, as decarbamoylsaxitoxin migrates slightly ahead of the new toxin (gonyautoxin-VII) to cathode in pH 8.4 buffer (Table 1).

Acknowledgments

We thank Mr L. Ph. Daneault (Department of Fisheries and Oceans, Fisheries Inspection Laboratory, Yarmouth, N.S.) for arranging the collection of this sample and also Captain E. Titus (Centerville, Digby Co., N.S.) for the actual sample collection.

The work at the University of Rhode Island was supported by HEW Grant FD-00619 and Sea Grant, University of Rhode Island R/D-5.

ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS. 1975. Paralytic Shellfish Poison, Biological Method (28), p. 319–321. *In* Official methods of analysis, 12th ed. (rev.) Washington, D.C.: Asoc. Offic. Anal. Chem.

BOURNE, N. 1965. Paralytic shellfish poison in sea scallops (*Placopecten magellanicus* Gmelin), J. Fish. Res. Board Can. 22: 1137–1149.

BUCKLEY, L. J., M. IKAWA, AND J. J. SASNER, JR. 1976. Isolation of *Gonyaulax tamarensis* toxins from softshell clams (*Mya arenaria*) and a thin layer chromatographic–fluorometric methods for their detection. J. Agric. Food Chem. 24: 107–111.

BUCKLEY, L. J., Y. OSHIMA, AND Y. SHIMIZU. 1978. Construction of a paralytic shellfish toxin analyzer and its application. Anal. Biochem. 85: 157–164.

FALLON, W. E., AND Y. SHIMIZU. 1977. Electrophoretic analysis of paralytic shellfish toxins. J. Environ. Sci. Health A12(9): 455–464.

GHAZAROSSIAN, V. E., E. J. SCHANTZ, H. K. SCHNOES, AND F. M. STRONG. 1974. Identification of a poison in toxic scallops from a *Gonyaulax tamarensis* red tide. Biochem. Biophys. Res. Commun. 59: 1219–1225.

1976. A biologically active acid hydrolysis product of saxitoxin. Biochem. Biophys. Res. Commun. 68: 776–780.

LOEBLICH, L. A., AND A. R. LOEBLICH. 1975. The organism causing New England red tides: *Gonyaulax excavata*, p. 207–224. *In* V. R. LoCicero [ed.] Proc. 1st Int. Conf. on Toxic Dinoflagellate Blooms. Mass. Sci. Technol. Found., Wakefield, Mass.

MEDCOF, J. C., A. H. LEIM, A. B. NEEDLER, A. W. H. NEEDLER, J. GIBBARD, AND J. NAUBERT. 1947. Paralytic shellfish poisoning on the Canadian Atlantic coast. Bull. Fish. Res. Board Can. 75: 32 p.

NEEDLER, A. B. 1949. Paralytic shellfish poisoning and *Gonyaulax tamarensis* J. Fish. Res. Board Can. 7: 490–504.

OSHIMA, Y., L. J. BUCKLEY, M. ALAM, AND Y. SHIMIZU. 1977. Heterogeneity of paralytic shellfish poisons. Three new toxins from cultured *Gonyaulax tamarensis* cells, *Mya arenaria*, and *Saxidomus giganteus*. Comp. Biochem. Physiol. 57c: 31–34.

PRAKASH, A. 1963. Source of paralytic shellfish toxin in the Bay of Fundy. J. Fish. Res. Board Can. 20: 983–996.

1967. Growth and toxicity of a marine dinoflagellate *Gonyaulax tamarensis*. J. Fish. Res. Board Can. 24: 1589–1606.

PRAKASH, A., J. C. MEDCOF, AND A. D. TENNANT. 1971. Paralytic shellfish poisoning in eastern Canada. Bull. Fish. Res. Board Can. 177: 23 p.

SCHANTZ, E. J. 1960. Biochemical studies on paralytic shellfish poisons. Ann. N.Y. Acad. Sci. 89: 843–855.

SCHANTZ, E. J., J. M. LYNCH, G. VAYVADA, K. MATSUMOTO, AND H. RAPOPORT. 1966. The purification and characterization of the poison produced by *Gonyaulax catenella* in axenic culture. Biochemistry 5: 1191–1195.

SCHANTZ, E. J., J. D. MOLD, D. W. STRANGER, J. SHAVEL, F. J. RIEL, J. P. BOWDEN, J. M. LYNCH, R. S. WYLER, B. REIGEL, AND H. SOMMER. 1957. Paralytic shellfish poison. VI. A procedure for the isolation and purification of the poison from toxic clams and mussel tissues. J. Am. Chem. Soc. 79: 5230–5235.

SHIMIZU, Y., M. ALAM, Y. OSHIMA, L. J. BUCKLEY, W. E. FALLON, H. KASAI, I. MIURA, V. P. GULLO, AND K. NAKANISHI. 1977. Chemistry and distribution of deleterious dinoflagellate toxins, p. 261–269. D. J. Faulkner and W. H. Fenical, [ed.] *In* Marine natural product chemistry (1977). Plenum Publishing Corp., New York, N.Y.

SHIMIZU, Y., M. ALAM, Y. OSHIMA, AND W. E. FALLON. 1975. Presence of four toxins in red tide infested clams and cultured *Gonyaulax tamarensis* cells. Biochem., Biophys. Res. Commun. 66: 731–737.

SHIMIZU, Y., L. J. BUCKLEY, M. ALAM, Y. OSHIMA, W. E. FALLON, H. KASAI, I. MIURA, V. P. GULLO, AND K. NAKANISHI. 1976. Structures of gonyautoxin II and III from the east coast toxic dinoflagellate, *Gonyaulax tamarensis*. J. Am. Chem. Soc. 98: 5414–5416.

SHIMIZU, Y., W. E. FALLON, J. C. WEKELL, D. GERBER, JR., AND E. J. GAUGLITZ, JR. 1978. Analysis of toxic mussels (*Mytilus* sp.) from the Alaskan Inside Passage. J. Agric. Food Chem. 26: 878–881.

Entrainment of Larval Fish by the Douglas Point Generating Station, Lake Huron, in Relation to Seasonal Succession and Distribution

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Larval fish were sampled by net in Lake Huron and the Douglas Point generating station throughout spring, summer, and early fall 1975. Dominance shifted from fourhorn sculpin (*Myoxocephalus quadricornis*) to rainbow smelt (*Osmerus mordax*) then to alewife (*Alosa pseudoharengus*) from late April to late September. Entrainment of the major species paralleled dominance and abundance observed in the lake, but yellow perch (*Perca flavescens*), brook stickleback (*Eucalia inconstans*), and slimy sculpin (*Cottus cognatus*) caught in the lake — each ranging from 5 to 25% of the total catch — were not entrained. Conversely, white sucker (*Catostomus commersoni*) was entrained but not captured in the lake. Size of individuals entrained, upper limit approx. 40 mm, paralleled size of individuals in the lake. Vertical distribution, and thus proximity to the submerged intake, greatly influenced entrainment rate.

Key words: larval fish, entrainment, power plant, distribution, abundance.

KELSO, J. R. M., AND J. K. LESLIE. 1979. Entrainment of larval fish by the Douglas Point generating station, Lake Huron, in relation to seasonal succession and distribution. J. Fish. Res. Board Can. 36: 37–41.

Nous avons échantillonné au filet des larves de poissons dans le lac Huron et à la centrale électrique de Douglas Point au printemps, en été et au début de l'automne 1975. De fin avril à fin septembre, la dominance est passée des chabots de profondeur (*Myoxocephalus quadricornis*) aux éperlans arc-en-ciel (*Osmerus mordax*) et enfin aux gaspareaux (*Alosa pseudoharengus*). Les espèces aspirées par la prise d'eau de la centrale montrent un parallélisme avec la dominance et l'abondance observées dans le lac, sauf que les perchaudes (*Perca flavescens*), les épinoches à cinq épines (*Eucalia inconstans*) et les chabots visqueux (*Cottus cognatus*) capturés dans le lac — chaque espèce représentant de 5 à 25% des prises totales — ne furent pas aspirés. Réciproquement, les meuniers noirs (*Catostomus commersoni*) sont aspirés, mais ne sont pas capturés dans le lac. La taille des individus aspirés, dont la limite maximale est d'environ 40 mm, se compare à celle des individus dans le lac. La distribution verticale et, partant, la proximité de la prise d'eau submergée affecte beaucoup le taux d'aspiration.

Received May 5, 1978
Accepted October 17, 1978

Reçu le 5 mai 1978
Accepté le 17 octobre 1978

OUR understanding of seasonal succession and patterns of abundance for free-swimming fish larvae is limited (Amundrud et al. 1974). With growing concern over entrainment mortality of fish larvae, better understanding of entrainment in relation to natural phenomena is needed.

There are approximately 140 power plants >10 MW in the Great Lakes basin (Anon. 1975). Marcy (1975) reviewed the effect of power plants upon larval fish but found only limited data that were restricted to the eastern coast of the United States. Teleki (1976) presented preliminary data for one generating station, Nanticoke, on Lake Erie. In this paper, we relate entrainment of larval fishes in a 200-MW nuclear generating station to the seasonal succession in species and abundance occurring at Douglas Point, Lake Huron.

Materials and Methods

The generating station, located between Goderich and Southampton, Ontario, operated at a relatively constant level during the study. The intake for cooling water is 600 m offshore at a depth of about 15 m and connects with the forebay by a submerged tunnel. Cooling water flow ranged from 21.6 to 24.8 m^3/s. Daily average temperature rise across the condenser ranged from 7.1 to 13.6°C.

From April 25 to September 20, 1975, at approximately 3-wk intervals, three simultaneous sampling programs were carried out. First, the intake and outfall were sampled by

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Imprimé au Canada (J5237)

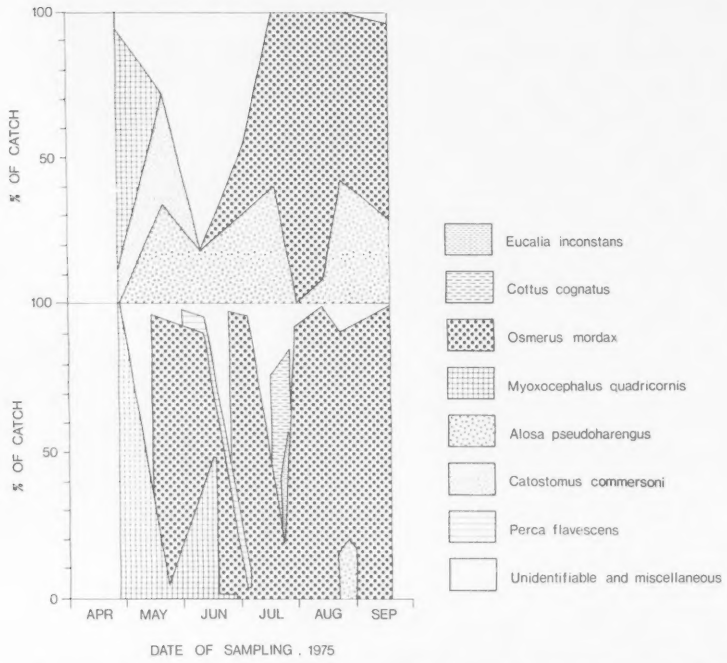

FIG. 1. Percent of total catch by larval fish species for samples collected in the Douglas Point generating station (*upper*) and at nearby locations (*lower*) in the lake, April–September 1975.

suspending nets mounted in a 1-m square aluminum frame in the mainstream. The nets were checked at 15- or 30-min intervals and between 1.0 and 3.7% of the daily condenser cooling water flow was sampled. Second, paired 0.5-m nets were pushed for 5 min at the surface in front of an outboard powered boat at each of 17 locations within 4 km of the generating station. Third, a 1.0-m net was towed for 5 or 10 min at depths of 0, 3, 5, 10, 15, and 20 m (where possible) at 5–9 locations up to 1.5 km from shore, perpendicular to it. Depth of sampling was determined from the wire angle and cable length and verified with a mechanical bathythermograph. All nets were made with 500-μm nitex mesh and equipped with a calibrated digital flowmeter. Each net had a 1-L screened collecting bucket.

Contents from each new tow were washed from the collecting bucket and preserved for laboratory sorting. Identifications from keys were verified by the Fish Identification Centre, National Museum of Natural Sciences, Ottawa, Ontario. Measurements of fish larvae were made using a calibrated ocular micrometer.

Results

Only 12 species were found in all the samples. Of these, seven were common (Fig. 1). Fourhorn sculpin (*Myoxocephalus quadricornis*), rainbow smelt (*Osmerus mordax*), and alewife (*Alosa pseudoharengus*) were the most abundant species. Whitefish (*Coregonus* sp.), freshwater drum (*Aplodinotus grunniens*), burbot (*Lota lota*), emerald shiner (*Notropis atherinoides*), and threespine stickleback (*Gasterosteus aculeatus*) were present but scarce. Dominance shifted from deepwater sculpin to smelt and then to alewife between mid-April and late-September. Entrainment of species by the generating station followed the pattern observed in the lake except for white sucker (*Catostomus commersoni*) which was entrained during May and early June but rarely captured in the lake (Fig. 1). Conversely, yellow perch (*Perca flavescens*), brook stickleback (*Eucalia inconstans*), and slimy sculpin (*Cottus cognatus*) were caught in moderate abundance, 5–25% by species of total catch, in the lake but were not entrained in power plant cooling waters. Alewife formed a greater proportion of larval fish entrained than they did in the lake.

Peaks in entrainment of larval fish paralleled peaks in abundance found in the lake (Fig. 2). Entrainment, as larvae per cubic metre, was generally up to 10 times greater than the density observed in the lake except for periods of low lake abundance in late June and early July. Since larvae were not always homogeneously distributed throughout the water column, lake surface tows did not adequately reflect density available for entrainment.

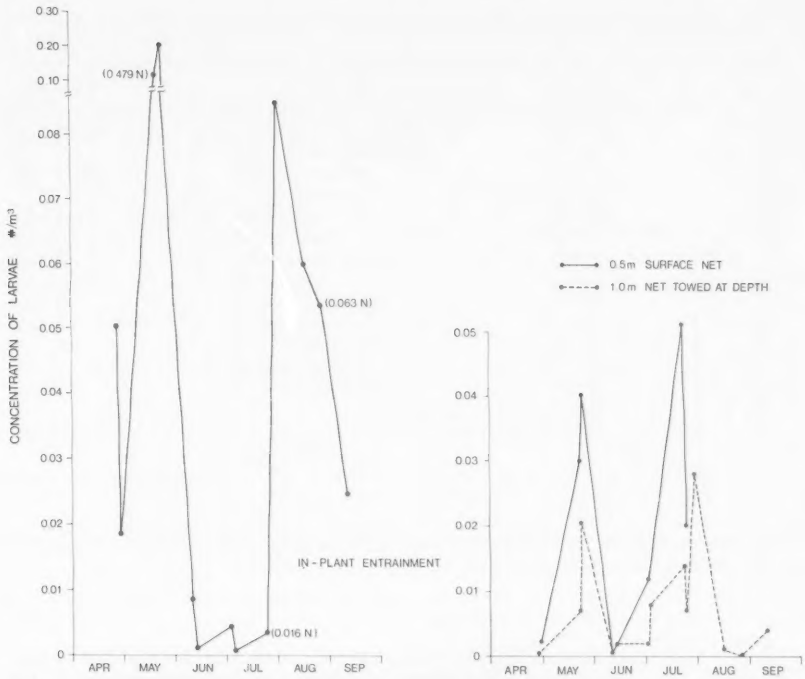

FIG. 2. Density of larval fish, all species, caught in the lake in surface tow nets, nets towed at depths between 0 and 20 m (*right hand panel*), and nets sampling in the Douglas Point generating station (*left hand panel*), April–September 1975.

Analysis of variance showed that when entrainment was high (Fig. 2) in the spring, densities were similar throughout the water column (Fig. 3). During July, when entrainment was low, greatest numbers of larvae were 5–10 m above the bottom ($F = 3.57^*$, df = 4, 12 and $F = 3.08^*$, df = 4, 16; *indicates $P < 0.05$). Entrainment rate increased again in late July, and when it decreased later in September vertical distribution was heterogeneous ($F = 3.47$, df = 4, 12) with greatest abundances near the water surface (Fig. 3).

On three occasions the sampling program was carried out at night. No differences in vertical distribution was found but density at night was greater ($F = 4.78^*$, df = 1, 26) during May but not in July or August. Generally, there appeared to be little difference between distribution and abundance during the day and night.

In addition to vertical heterogeneity in distribution, horizontal distribution was patchy. During late July, August, and early September, densities were greatest near shore (F values ranging from 2.94^* to 4.98^{**}; **indicates $P < 0.01$), decreasing with increasing distance from shore. At other times, no general pattern was apparent. Larval fish were always present near the generating station even on days (April 30 and June 9) when no larvae were captured elsewhere. The highest surface densities of larvae, 1.00–1.24 larvae per cubic metre, were found nearshore. The highest surface density found between 1 and 2 km from shore was only 0.07 larvae per cubic metre.

There were times when few larval fish were captured from the cooling waters (Table 1); however, densities of larval fish in the cooling waters frequently exceeded densities found in the lake (Fig. 2 and 3) at any depth. This phenomenon implies either inefficiencies in capture methods used for sampling larvae in the lake or selective entrainment by the generating station. Nevertheless, larval fish densities found in cooling waters were multiplied by cooling water use for the sampling date to calculate a hypothetical entrainment rate (Table 1). Daily entrainment of larval fish ranged from 3200 to 592 300. Using actual flow rates between sampling dates, the calculated possible total entrainment was 17.36×10^6 larval fish.

Although we examined most larvae caught from the cooling waters, any attempt to assess mortality and its causes was obviated since up to 100% of larval fish caught at the intake were dead and damaged (Table 1).

We compared sizes (standard length) of individuals captured in the lake and in cooling waters (Table 2). When species were represented by fewer than 10 fish,

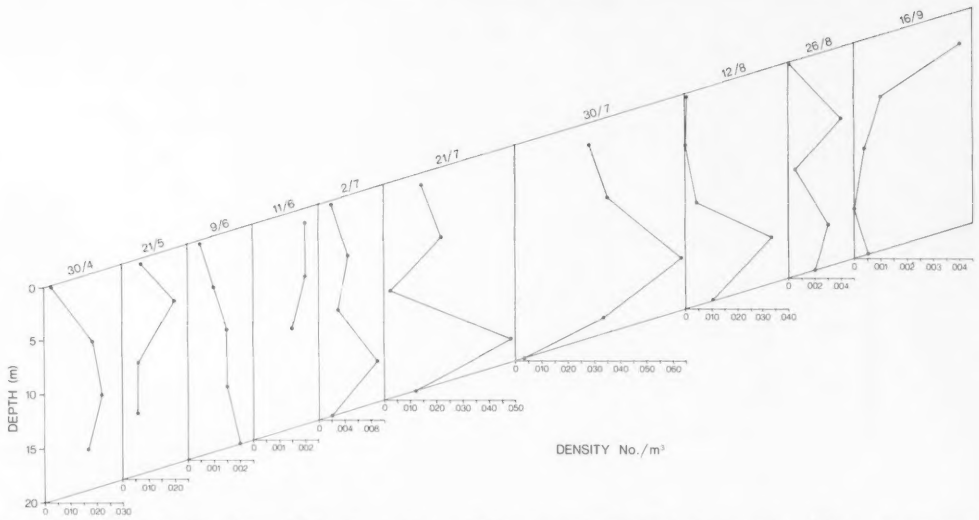

FIG. 3. Vertical distribution of larval fish, all species, caught in nets towed at depths between 0 and 20 m, all sampling locations, adjacent to the Douglas Point generating station, April–September 1975.

TABLE 1. Larval fish captured by metre net at intake and outfall of the Douglas Point generating station, 1975, and estimates of entrainment. Mortality was determined by examination of net captures.

Date, time of sampling 1975	Total larvae caught	Density no./m³	Hypothetical entrainment $\times 10^3$ no./d	% Dead at time of sampling	
				In	Out
Apr. 29, 30	78	0.036	44.6	76	91
May 21—Day	112	0.110	136.5	not recorded	
—Night	302	0.479	592.3	not recorded	
May 22—Day	269	0.221	273.5	97	92
May 21–22 Period	683	0.239	295.2	97	92
June 9–10 Period	11	0.0026	3.2	—	82
July 2–3 Period	9	0.0036	3.8	78	100
July 22–Day	2	0.0031	3.8	not recorded	
July 21/22 Night	29	0.0159	19.7	not recorded	
July 21–22 Period	31	0.0126	15.5	not recorded	
July 30	213	0.0843	104.2	94	29
Aug. 12	80	0.0598	73.9	61	Not samp.
Aug. 26—Day	96	0.0526	65.0	48	Nil caught
—Night	42	0.0582	71.9	10	(1 of) 100
—Period	138	0.0643	79.4	37	(1) 100
Sept. 16	35	0.0246	30.5	17	50

TABLE 2. Range in standard length (mm) for the dominant species found entrained in the power plant and captured in the lake, April–September 1975, Douglas Point, Lake Huron.

Date 1975	Species	Entrained	Lake
Apr. 29–30	*Myoxocephalus quadricornis*	9.0–15.0	8.8–13.4
	Catostomus commersoni	11.1–13.4	10.7–12.1
May 21–22	*Osmerus mordax*	4.2–6.9	4.3–11.8
	C. commersoni	6.0–16.7	5.8–14.0
June 9–11	All species	4.7–8.0	4.2–16.3
July 2	All species	4.5–14.1	2.9–14.9
July 21	*Alosa pseudoharengus*	4.5–4.6	3.4–9.1
	O. mordax	13.7–37.9	13.7–22.9
July 30	*A. pseudoharengus*	5.3–26.7	3.9–23.4
Aug. 12	*A. pseudoharengus*	10.4–40.6	5.0–20.3
Aug. 26	*A. pseudoharengus*	15.7–26.8	12.1–28.7
	O. mordax	29.8–34.0	30.3–37.7
Sept. 16	*A. pseudoharengus*	15.0–23.0	19.0–50.3
	All	4.2–40.6	2.9–50.3

data were grouped. The largest larval fish entrained was an alewife, 40.6 mm, and the smallest was a smelt, 4.2 mm. The largest larval fish captured in the lake was an alewife, 50.3 mm, and the smallest was an alewife, 2.9 mm. Entrainment did not appear to be size selective as sizes of larval fish entrained were generally similar to those in the lake.

Discussion

Power plants appear to entrain larval fish with relatively little bias. Differences in species do occur between larval fish entrained and those occurring naturally but the sizes are identical with the upper limit (approx. 40 mm) imposed by the screen size (approx. 1 cm) or larval fish behavior. Although the density of larval fish in cooling water frequently exceeded densities in the lake, the cause of this is unknown. Entrainment closely followed the local succession in fish species but since timing of reproduction and the structure of the community evolved depend upon habitat, the entrainment by power plants will reflect local ecological conditions.

Two findings have serious implications for existing and proposed thermal generating stations. First, power plants appear to concentrate larval fish and second, some selection by species occurs. The factors that contribute to these two phenomena are not known, but we presume that sampling gear selectivity, concentration by intake currents, or stress by the power plant which could affect the vulnerability of larval fish to the sampling gear are involved.

Available information (Marcy 1975) indicates that entrainment mortality is high (40–100%). Since we found net catches to be unsatisfactory for assessing mortality at Douglas Point, we are unable to estimate the direct loss from the estimated total entrainment.

The entrainment of only a few species of commercial or sport value should not remove the concern over effects of the once-through cooling process. Rather, this study demonstrates the need to treat a power plant as a component of a specific ecosystem and to examine entrainment in parallel with efforts to rehabilitate stocks.

Acknowledgments

W. H. Hyatt and P. Healey helped with all aspects of collection. Marine Sciences Directorate, Burlington, provided the boats used for sampling. Dr C. K. Minns helped with our inspection of the data. To these people and agencies we wish to express our thanks.

AMUNDRUD, J. R., D. J. FABERAND, A. KEAST. 1974. Seasonal succession of free-swimming perciform larvae in Lake Opinicon, Ontario. J. Fish. Res. Board Can. 31: 1661–1665.

ANON. 1975. An inventory of the thermal electric generating plants in the Great Lakes Basin. Int. Joint Comm. MS Rep. Windsor, Ont.

MARCY, B. C. JR. 1975. Entrainment of organisms at power plants with emphasis on fishes — an overview, p. 89–106. *In* S. B. Saila [ed.] Fisheries and energy production: a symposium. Lexington Books, Lexington, Mass.

TELEKI, G. C. 1976. Incidence and effect of once-through cooling on young-of-the-year fishes at Long Point Bay, Lake Erie: A preliminary assessment, p. 387–393. *In* G. W. Esch and R. W. McFarlane [ed.] Thermal ecology II. U.S. Tech. Info. Center, Energy Res. Dev. Admin., Oak Ridge, Tenn.

Deepwater Exchange Processes in the Saguenay Fjord

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SEIBERT, G. H., R. W. TRITES, AND S. J. REID. 1979. Deepwater exchange processes in the Saguenay Fjord. J. Fish. Res. Board Can. 36: 42–53.

Evidence is presented showing that the deep waters in the Saguenay Fjord are flushed at a rate that appears to be significantly higher than other sill fjords with comparable bathymetry. Interval waves in the St. Lawrence estuary, with magnitudes of up to 60m, provide a mechanism for bringing up dense water, semidiurnally, to the level of the seaward sill. Providing the density of the deep water in the fjord's outer basin is less than that at sill depth, a density flow develops and descends into the basin. Estimates of volume and kinetic energy fluxes of the plume suggest that, by itself, this is insufficient to explain the high flushing rates observed. Other processes, such as internal waves, which must be operative in carrying energy into the deep basin, are discussed.

Key words: estuaries, sill fjords, mixing, circulation, coastal

SEIBERT, G. H., R. W. TRITES, AND S. J. REID. 1979. Deepwater exchange processes in the Saguenay Fjord. J. Fish. Res. Board Can. 36: 42–53.

Nous démontrons qu'il y a débourdage des eaux profondes du fjord du Saguenay à un rythme qui semble nettement plus élevé que celui d'autres fjords à seuil de bathymétrie comparable. Des ondes internes dans l'estuaire du Saint-Laurent, d'amplitude allant jusqu'à 60 m, fournissent un mécanisme qui élève, deux fois pas jour, l'eau dense au niveau du seuil du côté de la mer. Pourvu que la densité de l'eau profonde dans le bassin extérieur du fjord soit moindre que celle qui existe à la profondeur du seuil, il se forme un écoulement de densité qui descend dans le bassin. Des estimations de volume et d'écoulements d'énergie cinétique de la plume donnent à croire que cet écoulement ne suffit pas à expliquer les taux de débourdage observés. Nous examinons d'autres processus, tels que les ondes internes, qui doivent entrer en jeu dans le transport de l'énergie dans le bassin profond.

Received July 12, 1978
Accepted October 18, 1978

Reçu le 12 juillet 1978
Accepté le 18 octobre 1978

WE have studied the nature and character of the physical replacement processes in the deep basins of fjords that have relatively shallow sills. Of special interest is the Saguenay Fjord in Quebec, which branches off the St. Lawrence estuary at the inner end of the Laurentian Channel (Fig. 1).

A number of researchers have focused on the circulation and exchange processes operative in sill fjords (e.g. Gade 1973; Long 1976; Stigebrandt 1976) but their models inadequately explain the observed oceanographic features of the Saguenay Fjord, even though general bathymetric similarity exists. Although some oceanographic aspects of the Saguenay Fjord were discussed by Drainville (1968), it was partly the finding of high concentrations of trace metals in the water and sediments of the fjord (Yeats and Bewers 1976; Loring 1976a, b) and high levels of mercury (Loring 1975; Loring and Bewers 1978) that placed new emphasis on obtaining a more detailed picture of the circulation and exchange processes active in the deep water of the fjord.

Printed in Canada (J5307)
Imprimé au Canada (J5307)

Oceanographic Data Base

Prior to 1961, only a few sporadic oceanographic measurements were available from the Saguenay Fjord. Oceanographic measurements taken in 1961 and 1962 and reported by Drainville (1968) consisted of temperature, salinity, and dissolved oxygen throughout the length of the fjord. Additionally, between 1961 and 1974 some 15 oceanographic

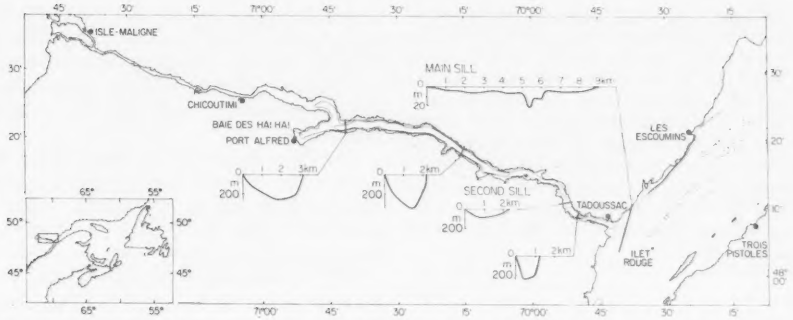

FIG. 1. Location of the Saguenay Fjord in relation to the Gulf of St. Lawrence and the St. Lawrence estuary.

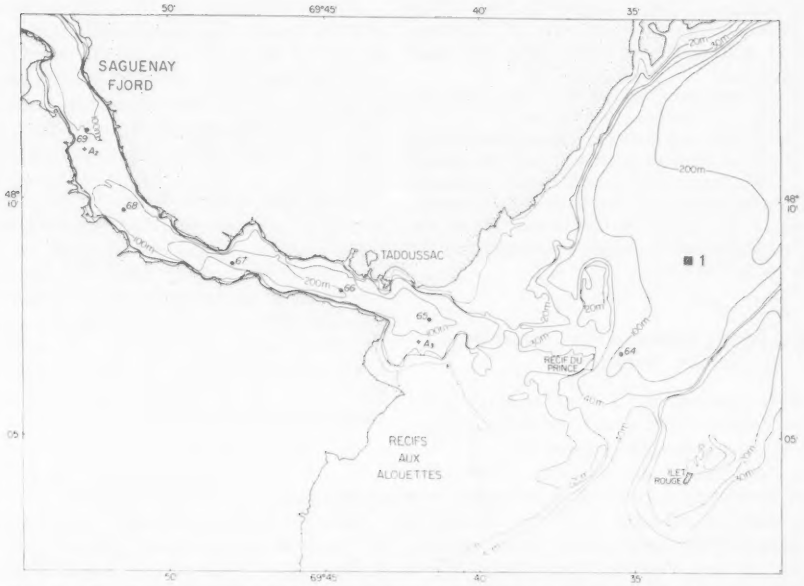

FIG. 2. Detail of the mouth of the Saguenay showing the grid and anchor station positions occupied in July 1975 and 1973 and the bathymetry of the sills.

sections, consisting of temperature, salinity, and at times, oxygen, were taken by federal agencies (Taylor 1975). More recently, Therriault and Lacroix (1975) described some observations made near the outer sill of the fjord which included measurements of chlorophyll. Work undertaken by the Bedford Institute of Oceanography in 1975 also focused on the lower reaches of the fjord, particularly the region between the two sills. A section line consisting of six stations (Fig. 2) was occupied 6 times. Each section (stations 64–69) took about 2 h to complete thus allowing six traverses within an M_2 tidal cycle. In addition, two anchor stations, each about 18 h long, were occupied near the two sills (Fig. 2). Measurements consisted of CTD (conductivity, temperature, depth) profiles and current velocity observations at selected depths using an Aanderaa CM4 current meter modified to integrate speed over a 30-s interval, and to give a continuous display of direction. The velocity measurements were decomposed into long- and cross-channel directions (343°T, 73°T for A2; 285°T, 15°T for A3). The velocity data were smoothed somewhat by fitting cubic splines to the vertical profiles. We estimate that the uncertainty in speed is $\pm 10\ \mathrm{cm \cdot s^{-1}}$ and in direction $\pm 20°$.

General Characteristics

Physiography and Bathymetry

The Saguenay Fjord, which varies in width from 1 to 4 km, exceeds 100 km in length. There is a large inner basin with a maximum depth of 275 m occupying some two thirds of the fjord. Seaward from this basin the bottom becomes

more irregular with a sequence of sills and basins. However, two principal sills separate the deep inner basin from the deep waters of the St. Lawrence estuary (Fig. 2). The shallowest of these sills is located at the mouth of the fjord, just seaward of Tadoussac where the water above it is barely 20 m deep. The second sill, located about 18 km upstream from the first, has a depth of water above it of about 80 m. The basin separating these sills has a maximum depth of approximately 250 m. Seaward of the mouth, depths in excess of 275 m are reached within a few kilometres. A more detailed description of the bathymetry is given by Drainville (1968).

Tidal Features

Within the Saguenay, the barotropic tide closely approximates a standing wave with a phase lag of <10 min between Tadoussac and Port Alfred near the inner end. The tidal range increases slightly toward the head of the fjord varying from a mean value of 4.0 m at Tadoussac to 4.3 m at Port Alfred. During spring tides the range increases to roughly 6 m.

Surface tidal currents near the mouth of the Saguenay are very strong with peak speeds reaching $3\ m \cdot s^{-1}$ in large tides. Internal tides, with a semidiurnal period, are known to be present in the St. Lawrence estuary near the mouth of the Saguenay (Forrester 1974), and speeds associated with them are comparable to the barotropic tidal currents. They appear to be generated by the interaction of the barotropic tide with the rapidly shoaling topography at the river end of the Laurentian Channel.

Seasonal and Yearly Variations in Temperature, Salinity, Density

The large-scale stratification of the Saguenay comprises a shallow zone (<25 m deep), overlying a deep, relatively homogeneous layer (Fig. 3 and 4).

For British Columbia fjords, Pickard (1961) distinguished two basic types of vertical profiles based on salinity in the near-surface zone. One type exhibits a well-defined surface layer which is nearly homogeneous, separated from a deep homogeneous layer by a halocline. In the second type, there is no homogeneous surface layer and the salinity increases with depth from the surface at a rate that decreases with depth. Drainville (1968) noted the existence of both types of structures in the Saguenay. In the data presented by Taylor (1975) it is also evident that both types of structures exist at one time or another. Although sampling in the upper 25 m was usually not sufficiently dense to define the structure precisely, it appears that when a homogeneous surface layer is present, it is usually <5 m in thickness. In light of the very high runoff into the Saguenay ($1–2 \times 10^3\ m^3 \cdot s^{-1}$) by comparison to the British Columbia fjords, it is somewhat surprising that a deeper and more pronounced homogeneous surface layer is not more frequently observed. Examples of the vertical–longitudinal distribution of salinity taken in July and August are shown in Fig. 3 and 4. From these it is noted that salinity in the near-surface zone increases relatively gradually throughout the inner two thirds of the fjord. However, large horizontal gradients exist near the mouth. During most of the year the surface zone has a distinctly different temperature from that of the deep waters, and exhibits a marked seasonal fluctuation.

The layer below 25 m depth within the inner basin is relatively uniform, with salinity increasing with depth and reaching values of 30–31‰ below 150 m. Temperatures within the deep layer of the inner basin are also relatively uniform with observed values always <5°C. In most cases, the water below 150 m depth has been observed to be <1.5°C. The coldest water has been observed most commonly to be in the inner part of the inner basin. Often the core is found at depths <150 m.

An examination of the data reported by Taylor (1975) reveals that significant changes in salinity and density of the deep water of the inner basin frequently occurred between cruises. While little can be concluded as to how rapidly these exchanges occurred, it appears that major replacements normally have occurred on at least an annual basis and minor replacements more frequently.

Conditions within the outer basin have been observed to be more variable than those within the inner basin. Of the 15 sections reported by Taylor, all but one show lower salinity and lower density water below 150 m depth in the outer basin compared to those at the same depth in the inner basin. On occasions, within the outer basin, the isopleths of salinity and density are seen to extend from 20 m to >150 m depth. As will be seen in the subsequent section, there are marked variations over a tidal cycle.

Dissolved Oxygen

Data for the Saguenay show a fairly wide fluctuation in dissolved oxygen concentration but on only one occasion out of eight cruises have values of <4 mL/L been observed (Fig. 4). It is common for values to exceed 6 mL/L at 250 m in the inner basin. The high dissolved oxygen content suggests that either its consumption rate is extremely low, or else the circulation and diffusion processes are relatively vigorous. By comparison to British Columbia fjords, which mostly do not have shallow sills (Pickard 1963), dissolved oxygen values appear to be substantially higher in the Saguenay. Similarly, values appear to be much higher in the Saguenay than for many of the Norwegian fjords where, for example, dissolved oxygen concentrations have been observed to drop to zero at times. The low dissolved oxygen concentrations in the Norwegian fjords have been attributed to the low flushing rate. While limited water exchanges tend to occur regularly on an annual basis, major flushing events occur at a much lower frequency with renewals as rare as once in 10 yr (Gade 1973).

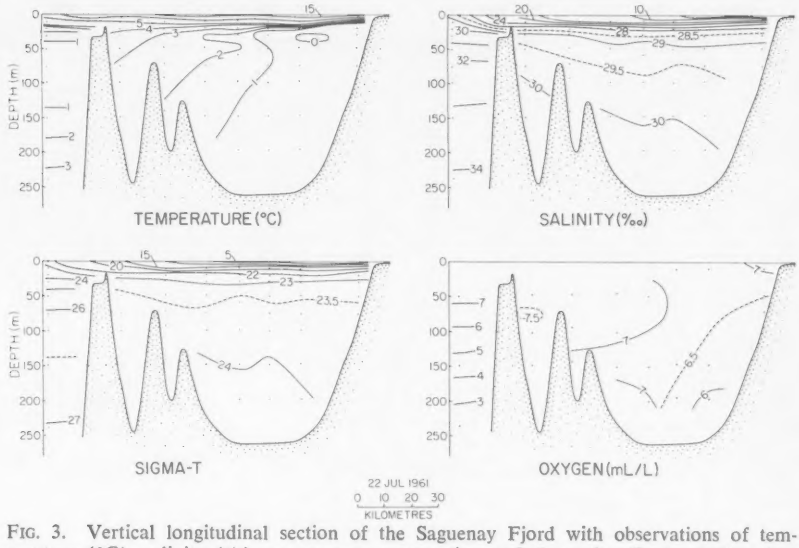

FIG. 3. Vertical longitudinal section of the Saguenay Fjord with observations of temperature (°C), salinity (‰), σ_t, oxygen concentration (mL/L) (after Taylor 1975); data taken July 22–23, 1961.

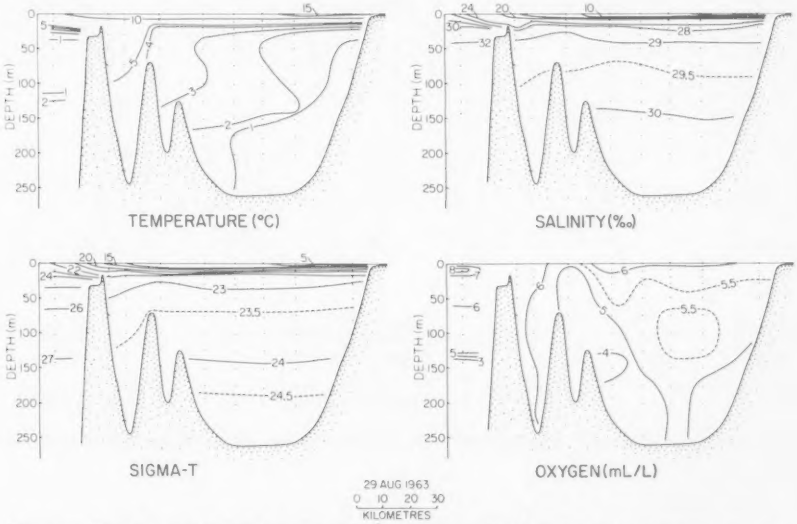

FIG. 4. Vertical longitudinal section of the Saguenay Fjord with observations of temperature (°C), salinity (‰), σ_t, oxygen concentration (mL/L) (after Taylor 1975); data taken August 29, 1963.

Since there is no reason to expect an abnormally low oxygen consumption in the Saguenay, the well-ventilated condition suggests that a relatively rapid exchange must take place between the deep water of the Saguenay and that of the upper euphotic zone either inside or outside the fjord.

Other Properties

Therriault and Lacroix (1975) presented data on chlorophyll *a* concentration taken at three stations within the Saguenay and one in the St. Lawrence estuary. Concentrations in the deep water in both the outer basin as well as in the area near the seaward end

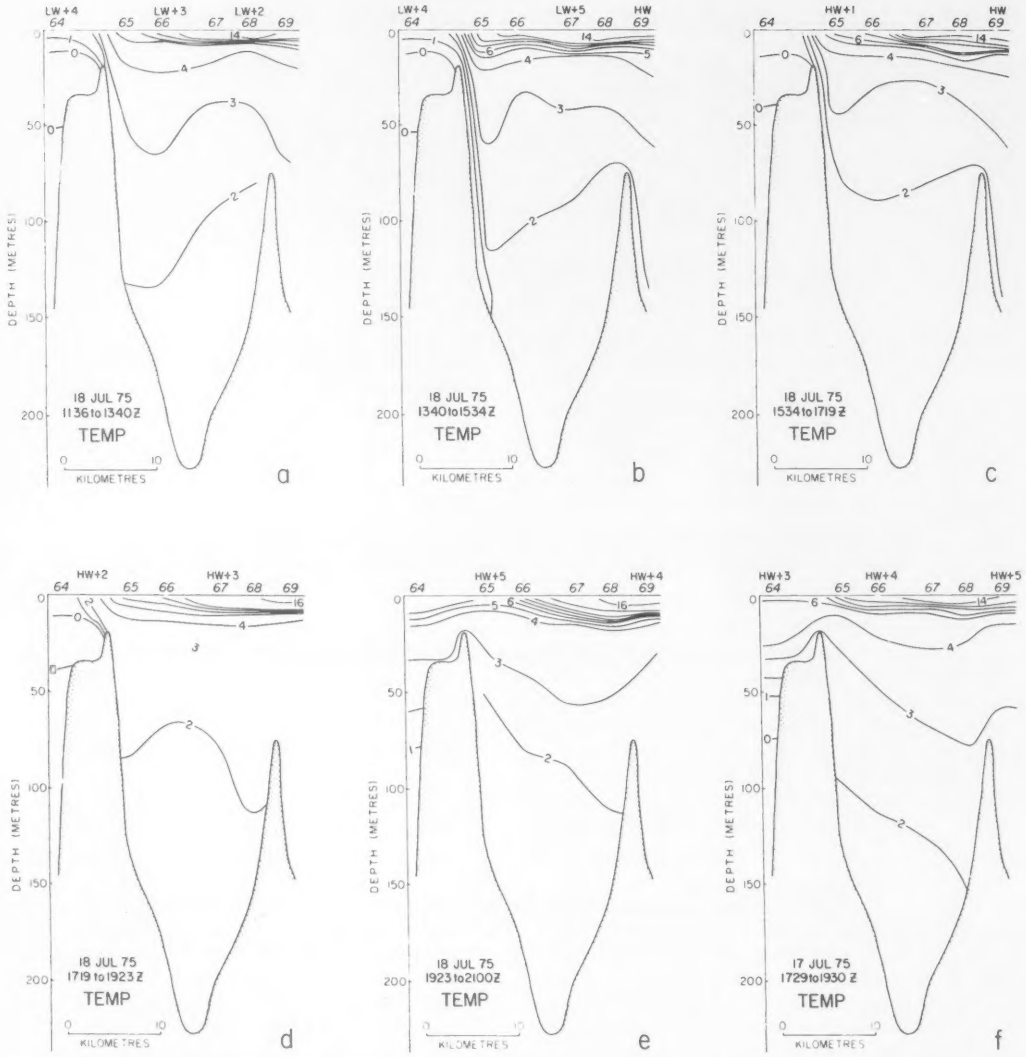

FIG. 5. Six longitudinal sections of temperature (°C) taken at various phases of the tide. The first five passes are during one tidal cycle.

of the inner basin exceeded 2 mg·m^{-3}. Since chlorophyll *a* can be produced only in the euphotic zone, which was estimated to be <10–15 m thick, its presence in the deep water must have been the result of advection and/or mixing.

Further indication of the replacement rate of the deep water in the inner basin can be derived from the distribution of manganese in suspended particulate matter measured in May and September 1974 (D. H. Loring personal communication). Over the 4-mo period between measurements, a well-defined zone of maximum concentrations had migrated inward and upward from about 175 m depth to <50 m.

Short-Term Variations in Properties

Repeated occupations of stations 64–69 (Fig. 2) showing the depth variations of temperature, salinity, and density isopleths at various phases of the surface tide (referenced to Tadoussac) are summarized in Fig. 5–7. The salinity distribution in the fjord is characterized by a thin (<15 m) surface layer with salinity

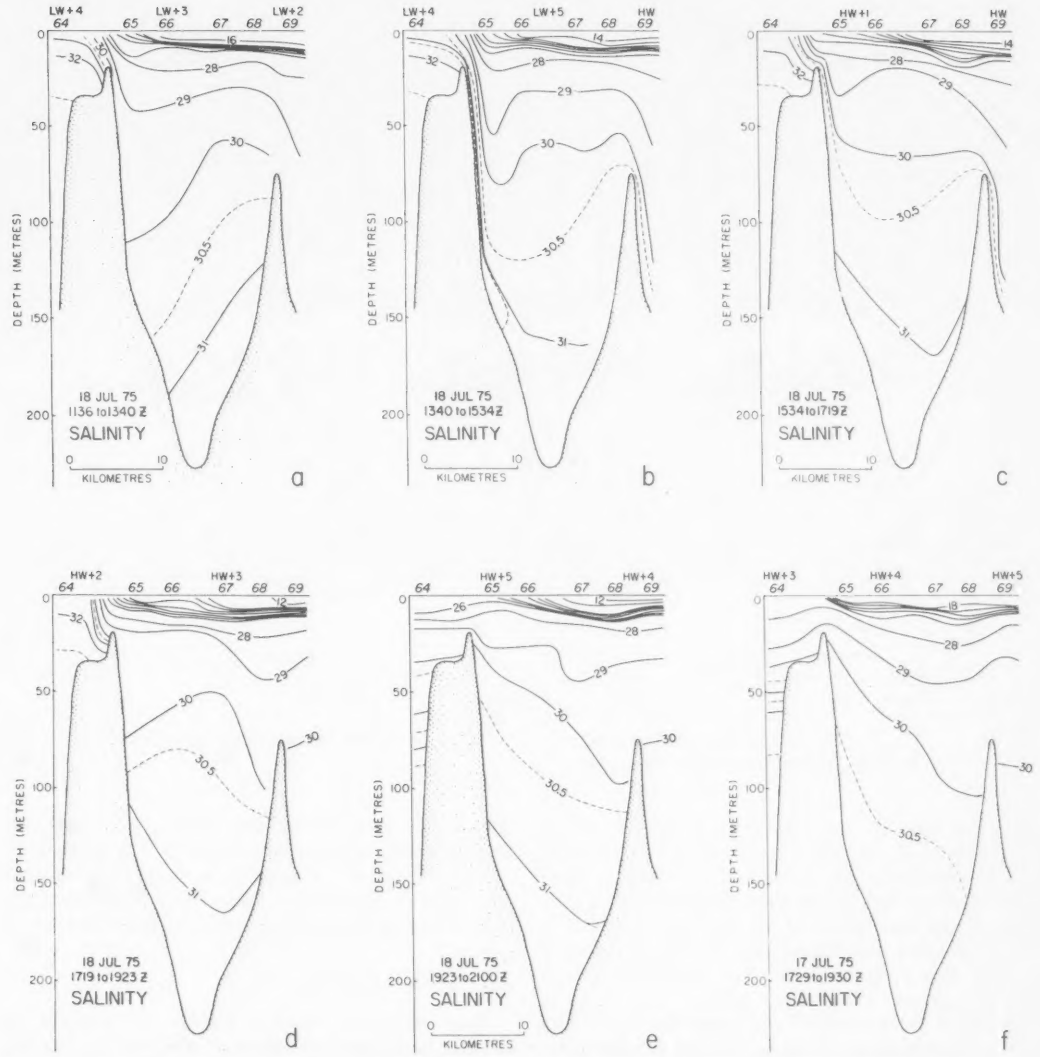

FIG. 6. Six longitudinal sections of salinity (‰) taken at various phases of the tide. The first five passes are during one tidal cycle.

<16‰ separated from a moderately stratified deep layer by a strong halocline (10‰·m^{-1}). The thickness of this brackish layer is greatest in the inner basin (Taylor 1975) and seems to disappear between stations 64 and 66.

In the initial stages of flood, surface salinity outside the fjord is close to 31‰ and similar to the deepwater salinity in the outer basin. The upper 0°C isotherm intersects the bottom at the outer sill — this isotherm is usually found at between 60 and 100 m in the St. Lawrence estuary (Forrester 1964). At peak flood (Fig. 5b, 6b), the large temperature and salinity changes at station 65 suggest an intrusion of cold (<1°C), saline (>31.5‰) water into the deep portions of the outer basin. The intrusion appears to take place in a thin (≃5 m) layer with the duration of the major pulse lasting no more than 3 h. Some water also appears to spill over the inner sill.

The general slope of the isopleths in the outer basin appears to change with the phase of the tide; sloping upward in the direction of flow on the upstream side of the sills. During the ebbing tide, the surface salinity

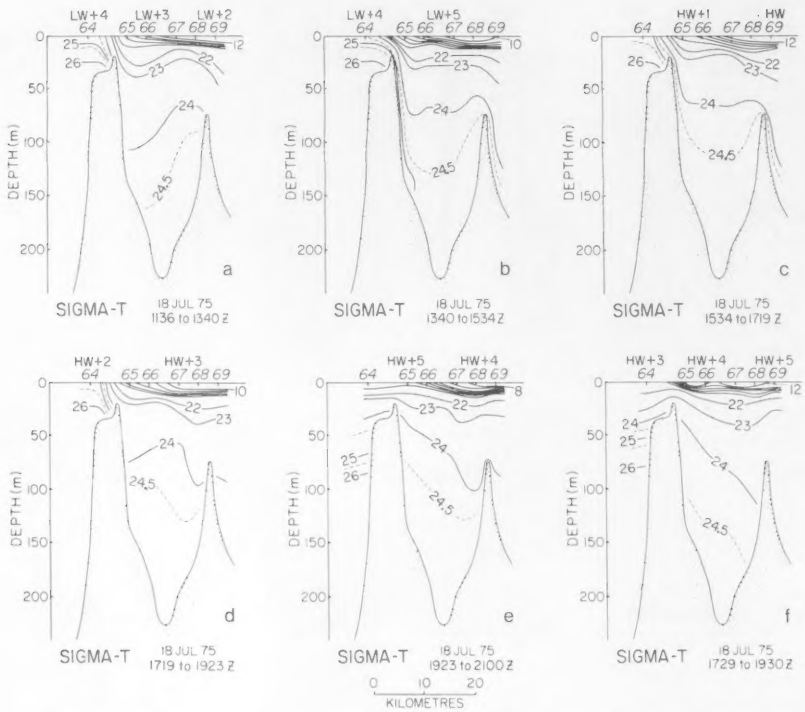

FIG. 7. Six longitudinal sections of density (σ_t) taken at various phases of the tide. The first five passes are during one tidal cycle.

outside the fjord is near 26‰ which is also the salinity at the base of the halocline inside the fjord. The 32‰ isopleth, which was near the surface at maximum flood is now at 80 m. Figures 6e and f compare salinity conditions at the same phase of the tide but separated by 25 h. Conditions over the sill are similar; however, at the later time (Fig. 6e), the 30‰ isopleth has been displaced upward in the water column and the basin below 150 m has been filled with water having salinity >31‰. The time scale of mixing processes in the upper 80 m of the water column must be fairly short as one would expect all the isopleths below sill depth to be displaced upwards by the deep intrusion. This displacement may, however, be masked by the large vertical excursion of water particles whose nature closely corresponds to an internal standing oscillation.

The data presented by Taylor (1975) were examined in order to relate time of station occupation with the phase of the tide at Tadoussac. Temperature, salinity, and density sections from three cruises are shown in Fig. 8. The wide station separation and nonsynoptic nature of the data (a section normally took 3 h or more to complete) does not permit accurate isopleth contouring; there is, nevertheless, good indication that the water was flowing inward and downward into the deepest part of the outer basin during a flooding tide. The similarity between Fig. 8 and 5–7 is particularly striking. There is a suggestion in both of these cases that some of the lower salinity water lying above the inward flowing water is also being advected downward.

ANCHOR STATION OBSERVATIONS

Time series of vertical profiles of temperature, salinity, and horizontal currents observed at the two anchor stations are shown in Fig. 9. For comparison purposes we have included Fig. 10 which shows the temporal variability in temperature and salinity measured July 3, 1973 at anchor station 1 located just seaward of the outer sill (Fig. 2). The isopleths varied in depth by as much as 60 m. There is evidence of a strong semidiurnal periodicity as well as some indication of shorter period oscillations. At sill depth (~20 m) temperature fluctuated from >6 to <1°C while salinity varied from <26 to >31‰. The highest salinity (and density) occurred near high water.

At station A3 the temperature and salinity series show a distinct tidal (semidiurnal) variation upon which are superimposed higher frequency fluctuations which seem to have periods longer than one hour, are

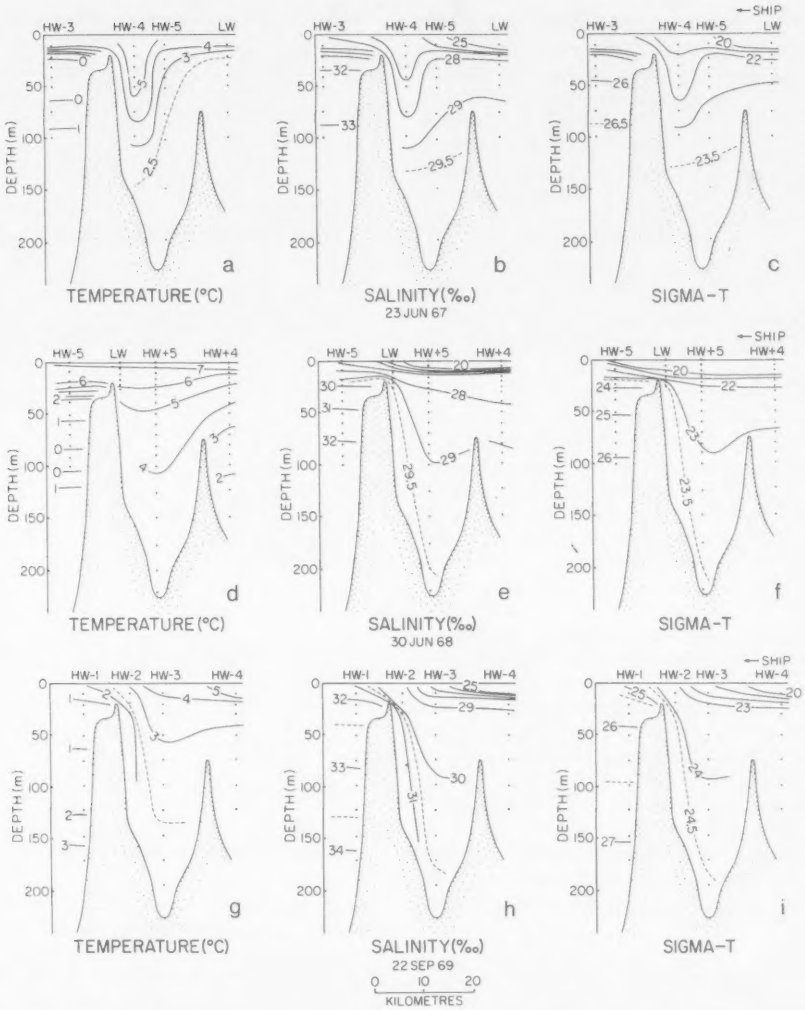

FIG. 8. Longitudinal sections of temperature, salinity, and density (σ_t) from cruises in 1967, 1968, and 1969.

in phase vertically, and have amplitudes increasing with depth. The internal semidiurnal variation in isopleth elevation lags the surface tide by approximately 90° and is asymmetric — there is an abrupt warming of the water column followed by a gradual cooling. The short period variations seem to occur in the lee of the frontal disturbance and last for at least 5 h.

At station A2, near the inner sill, the frequency content of the time series is not as obvious as at A3. The amplitudes are reduced and no distinct phase relationship is evident. The semidiurnal signal, evident at station A3, is absent or only weakly developed. However. there is some evidence of a 6-h variation.

Maximum flood currents at the inner sill occur between 30 and 50 m, and lead the surface tide by about 90° — suggesting that the tide approximates a standing wave. The duration of flood and ebb flow is unequal. However, an integration of velocity over depth and time (one M_2 period) leads to a net inward volume flux and hence the currents are probably not representative of the mean flow in the cross section. Near the outer sill, the currents are more variable than at the inner sill. The maximum flood flow nearly coincides with low water and takes place in a thin core centered at about 10–15 m. The cross-channel currents at both locations are fairly large and variable but consistent

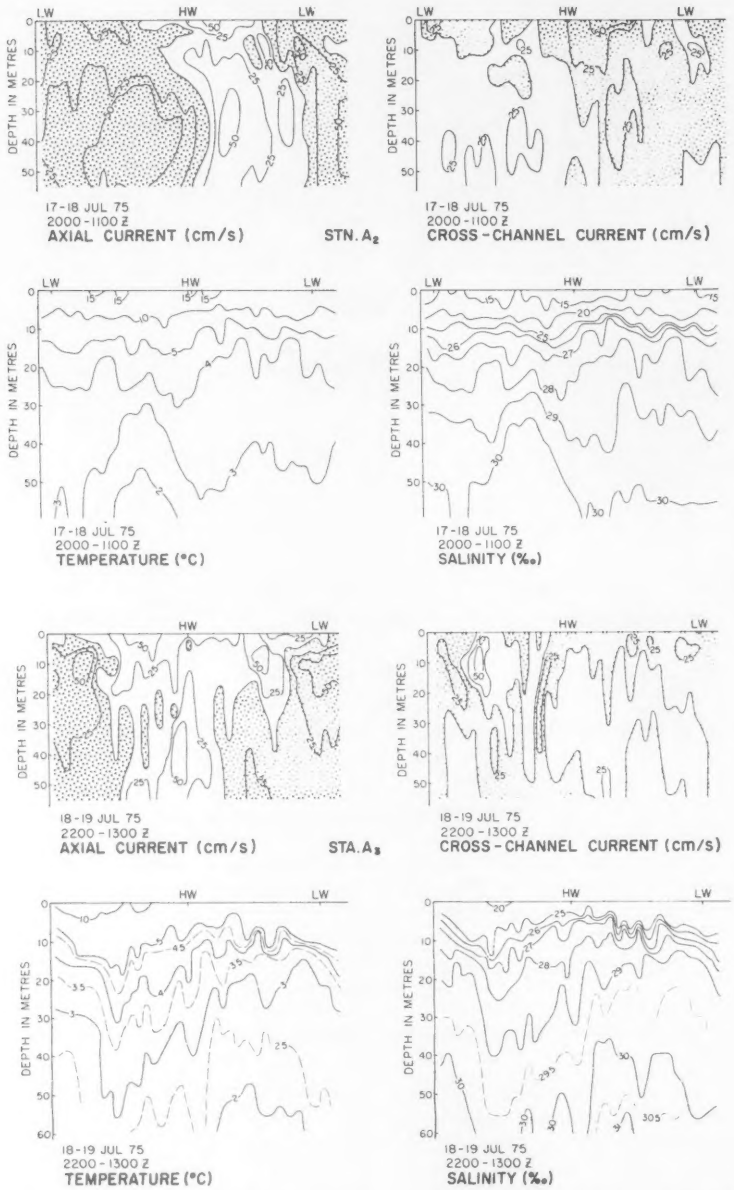

FIG. 9. Time histories of currents, temperature, and salinity observed at anchor stations A_2 and A_3, July 1975.

with the above. These cross-currents are probably due to boundary effects as the stations were not located in midchannel.

Discussion

In some fjords with shallow sills the deep water is exchanged by a series of spontaneous advective intrusions of dense water followed by a gradual reduction of density through vertical diffusion. From bathymetric considerations alone, one might expect that the replacement time for water in the deep basins of the Saguenay fjord would be measured in terms of months

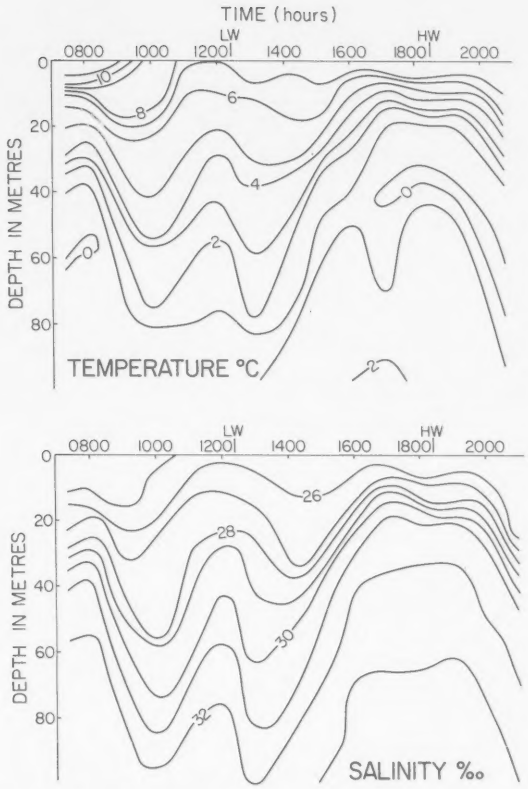

FIG. 10. Time series of temperature (°C) and salinity (‰) at station 1 July 3, 1973.

and years. However, from the available data, a time scale of days and weeks appear more likely. Evidence of cold dense water has been found at the surface, outside the main sill of the Saguenay, quite frequently. Aerial photographs and radiometer measurements by P. Vandall Jr. of the Bedford Institute (personal communication) have detected it by its lower turbidity and colder temperatures than surrounding water. The general region has also been identified from chemical and biological evidence as one of active upwelling (Steven 1974; Ingram 1975). The 1975 data indicate that the outer basin undergoes marked changes semidiurnally and, although appropriate data are not available for the entire length of the inner basin, it appears that significant variations also take place there at tidal frequencies.

The actual mechanism(s) that determines the appearance of dense water at the sill is not well known. Both Drainville (1968) and Therriault and Lacroix (1975) postulate that the dense water on the sill is St. Lawrence estuary surface water which flows into the outer basin to balance the volume and salt fluxes out of the Saguenay fjord. The temperature–salinity characteristics as observed in 1975 and other years, however, do not support this hypothesis. Figure 10, which shows the time–depth variations of temperature–salinity near Ilet Rouge, when compared to Fig. 5 and 6, makes it evident that the temperature–salinity characteristics near high water and 20 m closely correspond to those observed over the sill. This water ($T \simeq 1°C$, $S \simeq 31.5‰$), usually found at depths of 60–70 m, is Gulf of St. Lawrence intermediate water which undergoes little modification (the sill length is short compared to a typical tidal excursion) as it is lifted to sill level. Forrester (1974) and more recently Therriault and Lacroix (1976), showed that the temperature–salinity variations with M_2 frequency, as depicted in Fig. 10, are due to the generation, near the mouth of the Saguenay, of a progressive Poincare internal wave. The basic density distribution in the St. Lawrence estuary is such that the dominant wave is in the second vertical mode, i.e. the isopycnals in the upper 80 m experience vertical motions in phase with the surface tide with a maximum displacement at approximately 30 m. This is probably the dominant process by which dense, subsurface St. Lawrence estuary water is lifted to sill level.

Flows of dense fluid downslope and under relatively quiescent fjord water can be described in the manner of Ellison and Turner (1959), that is, mixing of plume and fjord water is accomplished mainly by entrainment. As the replacement time in the outer basin probably depends upon the equilibrium depth attained by the plume, the dynamics of the plume were studied using a slightly modified version of the stream tube model of Smith (1975). The dependent variables are integrated across the plume of cross-sectional area A. Thus, for a streamwise current u, the volumetric flux Q and momentum flux M are defined by

$$Q = \int\int u dA$$

$$M = \int\int u^2 dA$$

The model assumes a steady state, a geostrophic cross-stream balance, and the divergence of the downstream momentum flux is driven by the downslope component of gravity and retarded by bottom friction. The approximation to steady state can be justified on the basis that the time scale of the plume is at most 2 h which is less than the typical flood duration ($\simeq 6$ h).

Current and density profiles from station A3 and section plots were used to provide initial conditions for the model. The initial volumetric and momentum fluxes were estimated by assuming a plume thickness of 6 m and a width of 400 m.

Initial conditions and flow parameters were as follows:

Quantity	Value
Bottom slope	0.54×10^{-1}
Ambient stratification rate	$0.57 \times 10^{-7} \cdot cm^{-1}$

Initial velocity	$50\ cm \cdot s^{-1}$
Initial cross-sectional area	$2.4 \times 10^7\ cm^2$
Initial density contrast	$0.98 \times 10^{-3}\ g \cdot cm^{-3}$
Characteristic density	$1.01817\ g \cdot cm^{-3}$
Initial pitch angle	$\pi/2$

Once the initial conditions are set, the behavior of the plume is determined by friction and entrainment parameters, K and E, respectively. The data do not permit us to evaluate these and hence numerical experimentation was carried out with values of K and E chosen by trial and error such as to approximate the overflow of 1975. Numerical solutions were obtained by integrating the equations in the downstream direction starting with the above initial conditions until the plume separated from the bottom. It was found that the friction parameter K had a weak effect on the plume penetration depth; it was set equal to 1.15 m, which is equivalent to a nondimensional drag coefficient $C_D = 2.8 \times 10^{-3}$, and is consistent with estimates made by others (Edwards and Edelsten 1977) for flows with similar scales. The value of the entrainment parameter E was found to be small, on the order of 500 cm. The experiments of Ellison and Turner (1959) have shown that the entrainment parameter is a function of an overall Richardson number $Ri_0 = \Delta\rho g h/(\rho V^2)$, where h is the layer thickness, V the fluid rate. Using the observed layer thickness and other flow properties indicates that the stable conditions ($Ri_0 \simeq 1$) in the inflow region are responsible for the small values of E. This is to be considered as an order of magnitude estimate only as the data does not warrant a more detailed quantitative calculation. Within the parameter range considered here, calculations show that the speed of the plume at its maximum depth was about one half that at the source region.

Given the volume and kinetic energy flux in the plume we can estimate a replacement time for the basin below sill depth. The volume flux is on the order of $8.6 \times 10^{12}\ cm^3$/tide; compared to the volume of fluid below sill depth of $1.17 \times 10^{15}\ cm^3$ gives us an advective replacement time of 65 d. The actual replacement time due to this process could, however, be shorter. The initial momentum and volume fluxes were estimated using velocity data from anchor station A3; the actual velocity at the sill could, in fact, be much higher. This is in part based on visual information and the amount of water needed to sustain a tidal range of 4 m in the fjord. An increase of initial velocity to $250\ cm \cdot s^{-1}$, with other parameters remaining the same, leads to a Richardson number of 0.91×10^{-3} and hence a much larger entrainment coefficient; the maximum penetration depth is also reduced. A comparison of the July 17 and July 18 section data (Fig. 5 and 6) shows that a large portion of the deep basin has been filled with new water. Had the same phenomena occurred on subsequent flood tides, all of the basin would have been replaced in 2–3 d.

The plume kinetic energy input per tide is approximately $7.9 \times 10^{15}\ g \cdot cm^2 \cdot s^{-1}$. The change in potential energy per unit area in mixing a linearly stratified fluid column H m deep is given by $\Delta PE = 1/12\ g\ (\Delta\rho/\Delta z) H^3 = 7.18 \times 10^6\ g \cdot s^{-2}$ for $H = 130$ m. Thus, if all the kinetic energy were used for mixing we would obtain a replacement time of about 30 d. Thus, by itself, the stream tube model is insufficient to explain the high flushing rates observed. Other processes also must be operative in carrying energy into the deep basins. The most likely source of energy is tidal (the kinetic energy flux due to the barotropic tide is much larger than that due to the plume) but no transfer mechanism(s) can as yet be identified.

One possible mechanism could be the generation of internal waves by the scattering of the barotropic tides at abrupt changes in bottom topography, and their subsequent breaking along the sloping bottom topography or through shear instability. Using averaged density data from stations 65–69 and smoothed bottom topography we have calculated the internal wave (at M_2 frequency) ray paths emanating from critical zones (Baines 1974). The distribution of characteristics is complex due to multiple reflections from the bottom. However, it also shows that internal wave energy at tidal frequency can propagate into the deep portions of the basin to become a possible source for mixing.

Further quantification of the properties and flow characteristics along the slopes of the basins using moored instrumentation should provide major insight into the important operative mechanisms.

Acknowledgments

We gratefully acknowledge the advice and criticisms of our colleagues Drs D. Greenberg, D. Lawrence, B. Petrie, and P. Smith. The cooperation of the staff of the Drafting and Illustrations Group at BIO and crew of C.S.S. *Dawson* is also acknowledged.

BAINES, P. G. 1974. Generations of internal tides over steep continental slopes. Philos. Trans. R. Soc. London 227: 27–58.

DRAINVILLE, G. 1968. Le Fjord du Saguenay: Contribution à l'océanographie. Nat. Can. 95: 809–855.

EDWARDS, A., AND D. J. EDELSTEN. 1977. Deep Water Renewal of Loch Etive: A Three Basin Scottish Fjord. Estuarine Coastal Mar. Sci. 5: 575–595.

ELLISON, T. H., AND J. S. TURNER. 1959. Turbulent entrainment in stratified flows. J. Fluid Mech. 6: 423–448.

FARQUHARSON, W. 1962. Tides, tidal streams and currents in the Gulf of St. Lawrence. Canada Dep. Mines Tech. Surv. Mar. Sci. Branch, 76 p.

FORRESTER, W. D. 1964. A quantitative temperature-salinity study of the Gulf of St. Lawrence. Bedford Inst. Oceanogr. Rep. Ser. BIO-64-11, October 1964.

1974. Internal tides in the St. Lawrence Estuary. J. Mar. Res. 32: 55–66.

GADE, H. G. 1973. Deep water exchanges in a sill fjord: A stochastic process. J. Phys. Oceanogr. 3: 213–219.

INGRAM, R. G. 1975. Influence of tidal-induced vertical

mixing on primary productivity in the St. Lawrence estuary. Mem. Soc. R. Sci. Liege 6: 59–74.

LONG, R. R. 1976. Mass and salt transfers and halocline depths in an estuary. Tellus 28: 460–472.

LORING, D. H. 1975. Mercury in the sediments of the Gulf of St. Lawrence. Can. J. Earth Sci. 12: 1219–1237.

1976a. Distribution and partition of zinc, copper, and lead in the sediments of the Saguenay fjord. Can. J. Earth Sci. 13: 960–971.

1967b. Distribution and partition of cobalt, nickel, chromium and vanadium in the sediments of the Saguenay fjord. Can. J. Earth Sci. 13: 1706–1718.

LORING, D. H., AND J. M. BREWERS. 1978. Geochemical Mass Balances for Mercury in a Canadian Fjord. Chem. Geol. 22: 309–330.

PICKARD, G. L. 1961. Oceanographic features of inlets in the British Columbia mainland coast. J. Fish. Res. Board Can. 18: 908–999.

1963. Oceanographic characteristics of inlets of Vancouver Island, British Columbia. J. Fish. Res. Board Can. 20: 1109–1144.

STEVEN, D. M. 1974. Primary and secondary production in the Gulf of St. Lawrence. Marine Sciences Centre, Rep. No. 26, McGill University, Montreal, Quebec.

STIGEBRANDT, A. 1976. Vertical diffusion driven by internal waves in a sill fjord. J. Phys. Oceanogr. 6: 486–495.

SMITH, P. C. 1975. A stream tube model for the bottom boundary currents in the ocean. Deep-Sea Res. 22: 853–874.

TAYLOR, G. B. 1975. Saguenay River sections from fifteen cruises 1961–1974. Bedford Inst. Oceanogr. Data Ser. BI-D-75-2.

THERRIAULT, J. C., AND G. LACROIX. 1975. Penetration of the deep layer of the Saguenay Fjord by surface waters of the St. Lawrence Estuary. J. Fish. Res. Board Can. 32: 2373–2377.

1976. Nutrients, chlorophyll, and internal tides in the St. Lawrence Estuary. J. Fish. Res. Board Can. 33: 2747–2757.

YEATS, P. A., AND J. M. BEWERS. 1976. Trace metals in the waters of the Saguenay Fjord. Can. J. Earth Sci. 13: 1319–1327.

Periodicities in Atlantic Coast Striped Bass (*Morone saxatilis*) Commercial Fisheries Data[1]

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VAN WINKLE, W., B. L. KIRK, AND B. W. RUST. 1979. Periodicities in Atlantic Coast striped bass (*Morone saxatilis*) commercial fisheries data. J. Fish. Res. Board Can. 36: 54–62.

Atlantic Coast striped bass (*Morone saxatilis*) commercial fisheries data are examined for periodicities in the appearance of dominant year-classes using autocorrelation and spectral-analysis techniques. Results obtained using maximum entropy and classical Fourier spectral-analysis methods are compared. Statistically significant periodicities of approximately 20 yr and of 6–8 yr are common to the time series for most states and regions. Since the periodicities are neither very pronounced nor simple, it is difficult to isolate the causative factors, which are more likely to be density-independent environmental factors enhancing survival of the young than intrinsic characteristics of the life cycle of striped bass. The spectra for Maryland landings and Maryland landings per unit gear are nearly identical, suggesting that at least for Maryland the landings and landings-per-unit-gear data are approximately equally reliable as indices of stock size. The structure of the North Carolina time series is unique, which supports the opinion that this stock does not mix appreciably with Chesapeake and Hudson stocks. Impact assessments and monitoring programs should not be predicted on the expectation of pronounced or simple periodicities of 6 years or any other time interval in the appearance of dominant year-classes in Atlantic Coast striped bass populations.

Key words: autocorrelation analysis, commercial fisheries data, Fourier spectral analysis, maximum entropy spectral analysis, periodicities, striped bass

VAN WINKLE, W., B. L. KIRK, AND B. W. RUST. 1979. Periodicities in Atlantic Coast striped bass (*Morone saxatilis*) commercial fisheries data. J. Fish. Res. Board Can. 36: 54–62.

Les auteurs étudient les données de pêche commerciale de bar d'Amérique sur la côte de l'Atlantique en vue d'y déceler des périodicités dans l'apparition de classes d'âge dominantes, en se servant de techniques d'autocorrélation et d'analyses spectrales. Ils comparent les résultats obtenus par la méthode d'entropie maximale avec ceux de la méthode classique d'analyse spectrale de Fourier. Des périodicités d'environ 20 ans et de 6 à 8 ans, significatives à l'analyse statistique, sont communes à la série chronologique de données de la plupart des Etats et des régions. Comme les périodicités ne sont jamais très prononcées ni simples, il est difficile d'en isoler les facteurs responsables. Ces derniers sont tout probablement des facteurs ambiants indépendants de la densité et favorisant la survie des jeunes, plutôt que des caractéristiques intrinsèques du cycle biologique des bars d'Amérique. Le spectre des débarquements au Maryland et des débarquements par unité d'engin de pêche dans le même Etat est presque identique, ce qui donne à croire qu'au moins au Maryland, les données de débarquements et de débarquements par unité d'engin sont tous deux de bons indices de la taille des stocks. La structure de la série chronologique de données de la Caroline du Nord est unique, ce qui corrobore l'hypothèse que ce stock ne se mélange pas de façon appréciable à ceux de Chesapeake et d'Hudson. On ne devrait pas fonder les évaluations d'impact et les programmes de surveillance sur la probabilité de périodicités prononcées ou simples de 6 ans ou de tout autre intervalle de temps dans l'apparition des classes d'âge dominantes dans les populations de bars d'Amérique de la côte de l'Atlantique.

Received September 14, 1977
Accepted October 17, 1978

Reçu le 14 septembre 1977
Accepté le 17 octobre 1978

[1]Research sponsored by the Division of Biomedical and Environmental Research, U.S. Department of Energy, under contract W-7405-eng-26 with Union Carbide Corporation. Publication No. 1246, Environmental Sciences Division, ORNL.

Printed in Canada (J4983)
Imprimé au Canada (J4983)

COMMERCIAL fisheries data since the 1930s indicate substantial yearly fluctuations, superimposed on a longer-term increasing trend, in the size of Atlantic Coast striped bass (*Morone saxatilis*) populations. Commercial-landings estimates and landings-per-unit-gear estimates, whether analyzed by region or state, commonly vary by a factor of 3–4 (ratio of maximum value to minimum value) within a period of 10 yr (Koo 1970; USNRC 1975, Appendix B, p. B-154).

Koo (1970) discussed these fluctuations in the commercial fisheries data and the role of dominant year-classes in causing these fluctuations. He pointed out what appears to be "a distinct pattern of fluctuation with alternation of high and low landings occurring at fairly regular intervals of about six years" (p. 89). He concluded that while some density-dependent factors may well contribute to the cause of these fluctuations, density-independent factors that tend to enhance the survival of the young are likely operative. In recent years there has been considerable informal discussion to the effect that cognizance should be taken of this 6-yr cycle in the appearance of dominant year-classes in performing impact assessments and designing monitoring programs.

The major objective of this paper is to examine Atlantic Coast striped bass commercial fisheries data for the occurrence of regular periodicities, particularly an approximate 6-yr cycle, using autocorrelation and spectral-analysis techniques. A second objective is to apply the recently developed technique of maximum entropy spectral analysis (Burg 1975) to these striped bass time series and to compare the results with those obtained using the classical techniques of Fourier spectral analysis.

Description of Time Series Analyzed

The time series for the Hudson Bay Company's lynx catch in the MacKenzie District of Canada for the years 1821–1934 has been included as a reference case, since this time series has already been extensively analyzed (Bulmer 1974; Elton and Nicholson 1942; Finerty 1972; Moran 1949, 1953). The striped bass time series selected for analysis are commercial-landings (L) data and landings-per-unit-gear (L/G) data from individual states (i.e. Massachusetts, New York, Maryland, and North Carolina) and from larger regions as defined by the National Marine Fisheries Service (i.e. New England, Middle Atlantic, and Chesapeake). The L/G data are assumed to be a more reliable index of actual stock size than the L data. The striped bass time series vary in length from 22 (North Carolina L/G data) to 45 yr (Maryland L data).

Values for L/G (Table 1) were estimated using Koo's (1970) methodology. Since this methodology makes use of the cumulative total L over the duration of the time series, and since the time series considered in our paper include data since 1966 (the final year considered by Koo), the L/G values reported here for 1966 and earlier years differ somewhat from those reported by Koo (1970). Values for landings (L) for 1966 and earlier years are as in Koo (1970). Time series for both L and L/G have been included for Maryland and New York. The two series are of approximately the same length for Maryland (45 and 42 yr, respectively), but not for New York (44 and 25 yr, respectively).

Methods of Analysis

Logarithmic Transformation

Each time series was analyzed using the original data and the natural logarithm of the original data. Only the results using the natural logarithms are reported in this paper, although our findings were essentially the same using the untransformed data. Four reasons for using a logarithmic transformation are discussed by Williamson (1972): (1) relative changes in populations are most easily studied on logarithmic plots; (2) the logarithm of population size is more symmetrically distributed than the population size itself; (3) many populations are so variable that their variation can only conveniently be shown on a logarithmic plot; and (4) the change in the natural logarithm of the numbers of a population fits in most conveniently with the basic exponential and logistic theory of population dynamics. A fifth reason for using a logarithmic transformation in this case is to make the variances more homogeneous, since for these commercial fisheries data there is a tendency for the standard deviation to be proportional to the mean.

Detrending Analysis

Each time series was detrended using the regression model $\ln N(t) = a + kt$, where $N(t)$ is the index of population size (i.e. either L or L/G), t is time, and a and k are regression coefficients. The purpose of the detrending analysis was twofold. First, the slope (k) of this regression line may be equated to the rate constant in the exponential population growth model $N(t) = N(t_0)e^{kt}$. Thus, in a plot of $\ln N(t)$ vs. t, a slope significantly different from zero indicates that the population has been increasing (or decreasing) over the duration of the time series. Furthermore, the slope provides an estimate of the average annual relative rate of change, that is $e^k - 1.0$. Second, it is important in any method of spectral analysis to remove linear trends that extend throughout the time series. If not removed, such a trend will be interpreted as an infinitely long period, the power of which will tend to mask the periodicities of primary interest.

Autocorrelation Analysis

Let $X_1, X_2, \ldots, X_n$ be the terms of a time series. Autocorrelation analysis entails calculating serial correlation coefficients, r_k, using pairs of values X_i, X_{i+k} from the time series that are lagged by k terms (e.g. terms that are k years apart in this case) (see Box and Jenkins 1970, Equation 2.1.10). A graph of the lag k as abscissa and r_k as ordinate is called the correlogram, and it can provide considerable information about the internal structure of a time series (Kendall 1973). We recorded the largest negative and largest positive r_k values from the correlogram for each time series. In some cases there were several lags with approximately the same r_k value. The lag associated with the largest positive r_k value is generally the dominant period in the time series. The lag associated with the largest negative r_k value is generally the dominant period in the time series divided by 2.

TABLE 1. Striped bass commercial fisheries time series analyzed in this paper. Sources are Koo (1970) for the years 1930–66; Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Current Fisheries Statistics Publications for the years since 1966. State abbreviations used are MA (Massachusetts), NY (New York), MD (Maryland), and NC (North Carolina). New England Region (NER) consists of Maine, New Hampshire, Massachusetts, and Rhode Island (commercial fishing for striped bass is not permitted in Connecticut). Middle Atlantic Region (MAR) consists of New York, New Jersey, and Delaware. Chesapeake Region (CHR) consists of Maryland and Virginia. L/G is landings (lb) per unit gear. For Massachusetts, L/G represents landings (lb) per handline hook; for New York, L/G represents landings (lb) per fishing unit which includes pound nets, haul seines, drift gillnets, and fixed gillnets; for North Carolina, L/G represents landings (lb) per fishing unit which includes pound nets, haul seines, and fixed gillnets. L is recorded commercial landings of striped bass in thousands of pounds.

	MA	NER	NY		MAR	MD		CHR	NC	
Year	L/G	L	L	L/G	L	L	L/G	L	L/G	Year
1930		89	66		205	1228	614	1653		1930
1931		90	64		135	635	329	1116		1931
1932		42	32		52	434	313	1028		1932
1933		61	19		40	314	194	833		1933
1934		41[a]	28[a]		51[a]	333	242	642		1934
1935		22	37		62	928	735	1302		1935
1936		236[a]	85[a]		233[a]	1864	1510	2383		1936
1937		450	132		405	2011	1802	3016		1937
1938		301	139		311	1714	1294	2869		1938
1939		285	184		446	1729	1307	2692		1939
1940		147	169		382	1180	965	1839		1940
1941		183[a]	218[a]		400[a]	1223	967	2089		1941
1942		219	266		419	2508	1762	3286		1942
1943		216	317		514	2594[a]	1501[a]	3915[a]		1943
1944		341	504		799	2681	1241	4545		1944
1945		317	301		782	1545	528	3664		1945
1946		406	482		963	1615	482	3699		1946
1947	89	119	244	225	413	2338	653	4063		1947
1948	105	151	356	289	758	2650	817	5102		1948
1949	74	162	626	732	902	2629	808	4542		1949
1950	43	167	517	554	897	3038	916	5834	142	1950
1951	163	265	626	525	981	2336	682	4140	125	1951
1952	152	179	486	391	1141	2172	660	3413	114	1952
1953	110	193	482	466	1023	2303	727	3106	146	1953
1954	85	184	439	791	636	2108	688	3059	200	1954
1955	98	106	506	1641	629	2572	657	3466	156	1955
1956	105	98	395	1402	473	2150	594	3145	169	1956
1957	61	80	553	2445	701	1859	556	2788	124	1957
1958	54	95	398	2009	479	3105	1104	4422	232	1958
1959	62	120	538	2599	746	4349	1470	6446	210	1959
1960	68	211	731	3604	870	4409	1551	6687	189	1960
1961	86	397	910	5585	1252	5408	1816	7262	141	1961
1962	241	682	657	3837	1259	3979	1328	5923	190	1962
1963	202	582	673	2725	1474	3749	1277	6496	225	1963
1964	247	632	995	6275	2022	3300	1084	5189	258	1964
1965	235	531	740	6113	1533	2949	340	5162	146	1965
1966	318	843	1050	8990	1428	3347	968	6150	128	1966
1967	376	802	1630	12080	2023	4150	1200	5827	335	1967
1968	488	987	1551	8580	2059	4532	1264	6146	357	1968
1969	537	1182	1535	9279	1888	5088	1429	7759	252	1969
1970	648	1442	1338	10649	1615	3978	1133	5759	312	1970
1971	318	1276	1184	7342	1513	2743	680	3964	225	1971
1972			836			3186		5779		1972
1973			1674			4678				1973
1974						3383				1974

[a]Estimated by linear interpolation between the preceding and following year.

SPECTRAL ANALYSIS

The classical, discrete Fourier transform method (Box and Jenkins 1970; Jenkins and Watts 1968; Kendall 1973; Platt and Denman 1975) was used for each time series. This method represents a discrete time series as a sum of sine and cosine terms. The Burg (1975) maximum

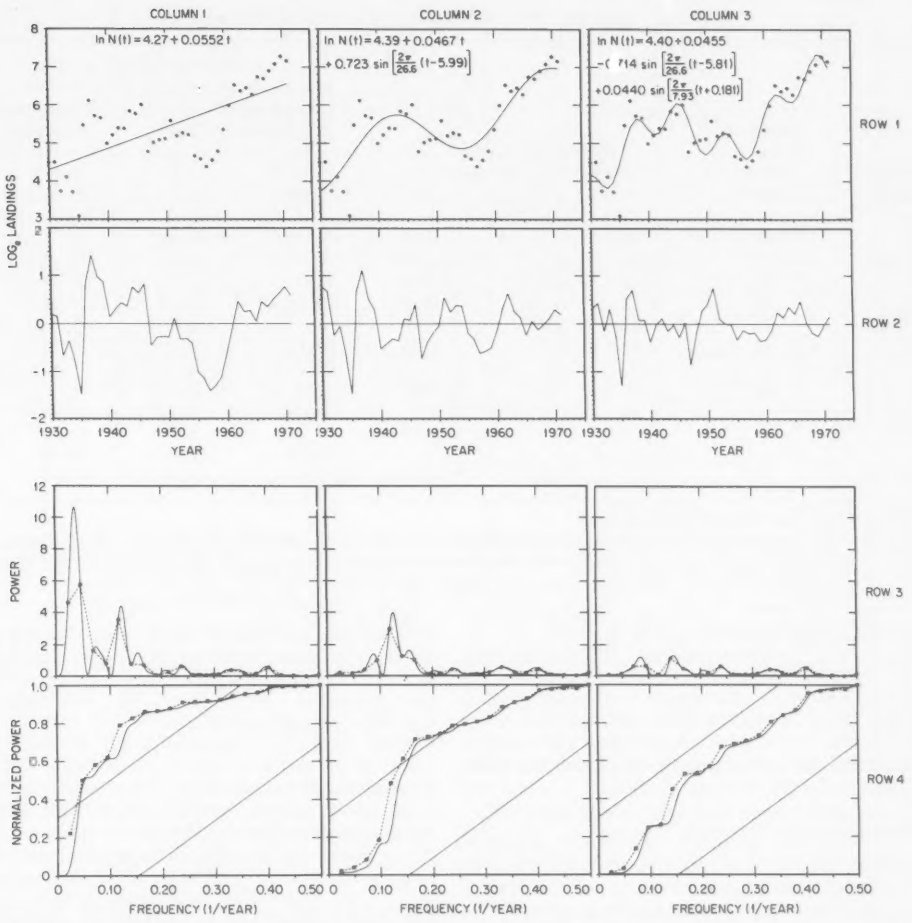

FIG. 1. Example illustrating the methodology chosen to identify statistically significant peaks in a frequency spectrum. The time series used is the striped bass (*Morone saxatilis*) commercial landings for the New England Region.

entropy method was also used. This method is based on the maximization of a function that gives a measure of one's ignorance in the intervals where data are not available (Ables 1974). Kirk et al. (1979) provide a comparison of these two methods of spectral analysis and point out the following three differences. First, Fourier spectral analysis (FSA) assumes a zero extension of the data and uses data windows (Jenkins and Watts 1968, p. 48–50), whereas maximum entropy spectral analysis (MESA) minimizes the assumptions about unavailable data and does not use data windows. Second, the longest period predicted by FSA is equal to the length of the time series, whereas MESA, in some cases, can predict periods longer than the length of the time series. Third, the power in the Fourier spectrum is proportional to the height of the peaks, while the power in the maximum entropy spectrum is proportional to the area under the curve.

The determination of the number of coefficients (denoted M) that will produce the best maximum entropy spectrum is one of the major unsolved problems in MESA (Burg 1975; Kirk et al. 1979). In general, when one uses a very small number for M the resulting spectrum is too smooth and may have unresolved peaks, that is, two or more true peaks that appear in the spectrum as a single peak. On the other hand, choosing M close to the total number of data points may result in a spectrum with too many spurious peaks, that is, peaks indicating periodicities that are not actually present in the time series. A common guideline is to choose M close to half the total number of data points. An alternative guideline is to use the Akaike final prediction error criterion (Ulrych 1975), which involves choosing that value of M that will minimize the final prediction error. Frequently, this value of M yields a threshold spectrum above which the spectrum is significantly sharper and better resolved than for lesser values of M. We used both of these guidelines, in combination with reference to the Fourier

TABLE 2. Summary of the detrending and autocorrelation analyses.

Description of time series[a]	Length of time series (years)	Detrending analysis[b]			Autocorrelation analysis: Largest negative serial correlation coefficient		Autocorrelation analysis: Largest positive serial correlation coefficient	
		r^2	k	P	Lag, k (years)	r_k	Lag, k (years)	r_k
Lynx	114	0.004	0.00256	0.48	5	−0.62	10	+0.60
MA; L/G	25	0.58	0.08	0.0001	9	−0.45	18–22	+0.2
NER; L	42	0.48	0.055	0.0001	11	−0.42	24–25	+0.3
NY; L	44	0.82	0.081	0.0001	11, 16–17	−0.26	37–39	+0.16
NY; L/G	25	0.92	0.16	0.0001	14	−0.038	6, 18	+0.2
MAR; L	42	0.71	0.07	0.0001	10–11	−0.2	23–24	+0.16
					17	−0.3		
MD; L	45	0.63	0.04	0.0001	4	−0.22	7	+0.10
MD; L/G	42	0.16	0.02	0.01	9–10	−0.33	22–24	+0.24
CHR; L	43	0.65	0.041	0.0001	10	−0.2	22–24	+0.1
					27–28	−0.25	37–38	+0.2
NC; L/G	22	0.45	0.03	0.0007	2, 7	−0.4	4–5, 9	+0.2

[a]See Table 1 for definition of abbreviations.

[b]Each time series was detrended using the regression model $\ln N(t) = a + kt$, where $N(t)$ is the index of population size, and t is year. r^2 is the coefficient of determination, k is the slope of the regression line, and P is the probability that the true slope is 0.0.

spectrum, in deciding which value of M to select.

Although it is not without problems, MESA is in many ways superior to the traditional Fourier transform for frequency analysis of time series because it minimizes implicit assumptions about unavailable data, does not distort the measured values with a data window, and gives sharper resolution of the spectrum, especially when the time series is short (Rust et al. 1976; Kirk et al. 1979).

STATISTICAL SIGNIFICANCE OF PEAKS

Three methods were used to test for the significance of a peak in a frequency spectrum. These three methods are briefly described below, using the striped bass L time series for the New England Region as an example (Fig. 1). The first method was Fisher's periodogram test (Fuller 1976, p. 283–285), which tests the largest ordinate value in the periodogram against the average of all the ordinates. (The periodogram of a time series is defined as a discrete Fourier approximation to the frequency spectrum with ordinates computed only at the fundamental frequency and its harmonics; see Fig. 1, Row 3, dashed lines). The calculated ratio of the largest ordinate to the average of all the ordinates was compared with tabulated values for this ratio at a probability level of 0.05. The main shortcoming of this method is that a true period may be somewhere between the ordinates in the periodogram, and thus, the continuous Fourier spectrum was also calculated (Fig. 1, Row 3, solid lines).

The second method was the cumulative periodogram test (Fuller 1976, p. 285), which tests the cumulative periodogram (Fig. 1, Row 4, dashed lines) or the cumulative Fourier spectrum (Fig. 1, Row 4, solid lines) against the cumulative distribution of a uniform distribution. To provide perspective, white noise would give a cumulative periodogram that would fall on the straight line running from (0.0, 0.0) to (0.5, 1.0) in Fig. 1, Row 4. We used 95% bounds, shown in the figure as parallel diagonal lines, for the cumulative periodogram test and accepted a peak as being statistically significant as long as it resulted in the cumulative periodogram (or cumulative Fourier spectrum) passing outside these 95% bounds.

If the largest peak was statistically significant as determined by the first two methods, a sine wave with a period equal to the period of the significant peak (as determined by maximum entropy spectral analysis) was added to the detrending regression equation discussed above, namely $\ln N(t) = a + kt$. Then the entire spectral analysis was repeated starting with the expanded regression model (Fig. 1, Row 1) and detrending the time series (Fig. 1, Row 2). The third method used to test for the significance of a peak in a frequency spectrum entailed using the standard F-test to determine whether the additional term in the regression model was statistically significant (at the $P = 0.05$ level).

This three-method procedure was repeated with each time series until the highest peak remaining in the spectrum was not statistically significant. In the case of the New England Region time series, this point was reached after first removing the peak with a period of 26.6 yr (Fig. 1, Column 2) and then removing the peak with a period of 7.93 yr (Fig. 1, Column 3).

Results and Discussion

LYNX

The slope (k) of the regression line for the lynx time series (Table 2, Fig. 2) does not differ significantly from 0.0, suggesting that there was neither a long-term increase or decrease in the size of the lynx population in the MacKenzie District during the 114-yr period. Regular population fluctuations with an apparent period

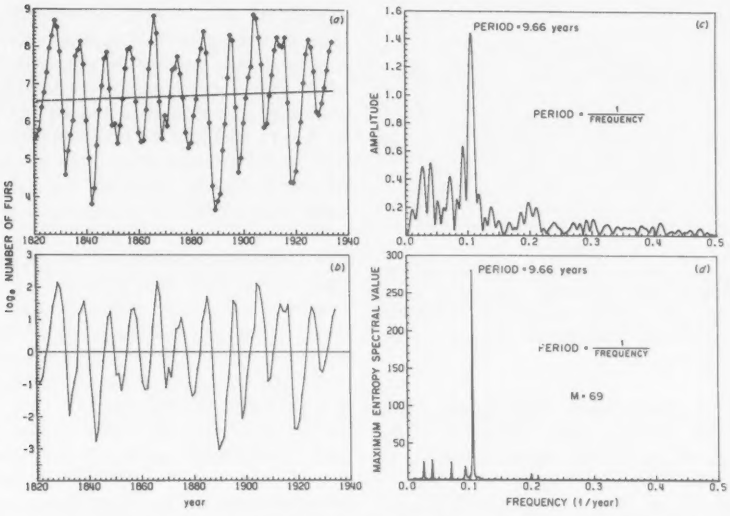

FIG. 2. Results for the lynx population in the MacKenzie District of Canada: (a) plot of the 114-yr (1821–1934) time series with the linear trend line drawn in; (b) plot of the detrended data (i.e. residuals); (c) Fourier spectrum of the residuals; and (d) maximum entropy spectrum of the residuals.

of approximately 10 yr are evident in Figs. 2a and 2b. The largest positive serial correlation coefficient (r_k) occurs with a lag of 10 yr, while the largest negative r_k value occurs with half that lag at 5 yr (Table 2, under autocorrelation analysis).

Both the Fourier and maximum entropy spectra (Fig. 2c and 2d) reinforce the results of the autocorrelation analysis (Table 2) and the impression created by just looking at the time series (Fig. 2a and 2b). The single statistically significant peak in both the Fourier and maximum entropy spectra corresponds to a period of 9.7 yr (Fig. 2c and 2d). As expected, the maximum entropy spectrum (Fig. 2d) is similar to the Fourier spectrum (Fig. 2c), although the sharper resolution obtained with MESA is clearly evident. The estimate of the dominant period of 9.7 yr is in agreement with those obtained by others (Bulmer 1974; Elton and Nicholson 1942; Finerty 1972; Moran 1953).

STRIPED BASS: AUTOCORRELATION ANALYSIS

The slope of the regression line is significantly greater than 0.0 ($P \leq 0.01$) for the striped bass time series for all states and regions (Table 2). This increase in the size of the striped bass stocks along the Atlantic Coast has been reported previously (e.g. Koo 1970; McHugh 1972). Factors influencing this increase, however, are not known, although Mansueti (1961) suggests that it may be due to the striped bass taking advantage of increased nutrient loads in its nursery areas in Chesapeake Bay and elsewhere. The rate of population growth appears to have been greatest for New York, with an average annual relative rate of increase of 17% per year as indicated by the LG time series. The average annual relative rate of increase for all other states and regions has been in the range of 2–8% per year.

The periods indicated by autocorrelation analysis are generally consistent with those indicated by spectral analysis. In other words, the lag associated with the largest positive r_k value and two times the lag associated with the largest negative r_k value (Table 2) generally corresponds to a statistically significant peak in the Fourier spectrum.

Two other results of the autocorrelation analysis merit comment. First, the absolute values of the negative and positive r_k values in Table 2 are uniformly lower than the r_k values for the lynx time series. Second, the lag associated with the r_k values for the striped bass time series commonly cover an interval of years (e.g. 18–22 yr for the largest positive r_k value for the Massachusetts LG time series; see Table 2), as opposed to a single year as for the lynx. Although the striped bass time series are in general only one third as long as the lynx time series, these two results suggest that there is more noise in the striped bass series than in the lynx series and that the actual periodicities in the striped bass series are less pronounced and less regular.

SPECTRAL ANALYSIS

Comparison of the maximum entropy spectra for the striped bass time series (Fig. 3) illustrates similar-

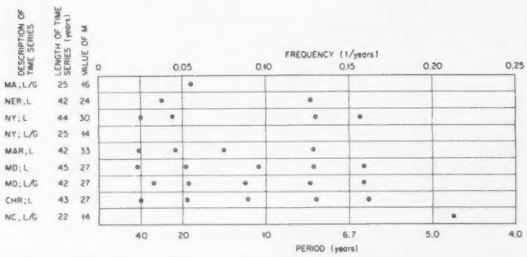

FIG. 3. Periods of the peaks in the maximum entropy spectra corresponding to the statistically significant peaks in the Fourier spectra for various striped-bass, detrended time series. See Table 1 for abbreviations used in the description of the time series.

ities and differences among states and regions. With the exception of the North Carolina time series, the common occurrence of statistically significant peaks in the interval of 18–23 yr (or 18–27 yr, if New England L are included) is evident. In addition, there is a common occurrence of statistically significant peaks in the interval of 6–8 yr (or 5–9 yr, if New York LG are included). Excluding North Carolina, the periodicities of approximately 20 yr are more pronounced for time series from the middle and southern part of the Atlantic Coast than from the northern part.

We have no ready explanation of what factors may account for the occurrence of an approximate 20-yr period, and, in fact, with additional data, this period may no longer appear to be so dominant. There are no aspects of the life cycle of striped bass that are consistent with a period of approximately 20 yr. Assuming a striped bass population operating on the right limb of a Ricker reproduction curve (Ricker 1975), and assuming that the great majority of eggs are spawned by 4–6 yr olds in the Chesapeake system and by 5–7 yr olds in the Hudson River, one would predict a period of approximately 10–12 yr, but not 20 yr. This comment also applies to explaining a 6–8-yr cycle based on the striped bass life cycle.

We agree with Koo (1970) that to ascertain the causes of any of these periodicities, we must consider density-independent environmental factors, such as temperature and freshwater flow, that are known to influence survival of young-of-the-year life stages directly and indirectly. However, we emphasize that since the periodicities are neither very pronounced nor simple, it will be difficult to isolate the causative factors. Furthermore, to be of predictive value it would be necessary to show that the causative factors themselves directly or indirectly have periodicities of approximately 20 yr or 6–8 yr and that these periodicities are in phase with those of the striped bass.

MARYLAND

The time series for Maryland L (Fig. 4) and Maryland LG (Fig. 5) are presented in more detail in order to evaluate the effect of refining the index of population size by using L/G and not just L, and in order to provide a second comparison of Fourier and maximum

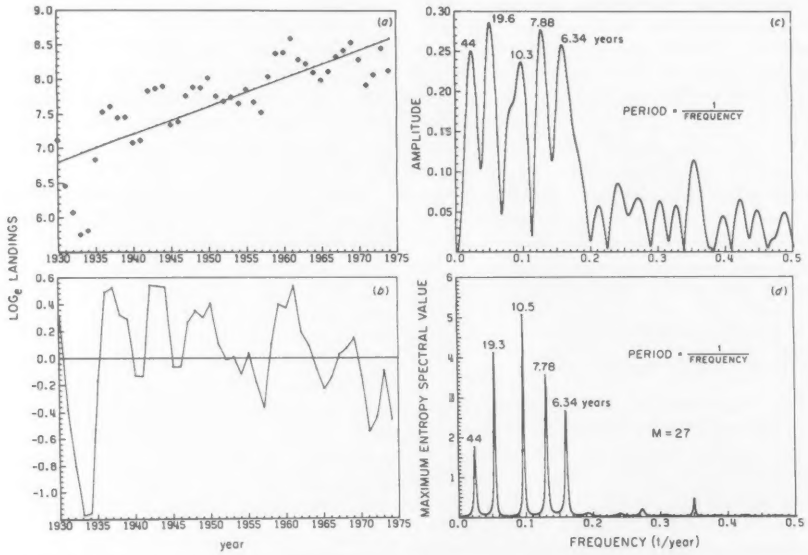

FIG. 4. Results for Maryland striped bass commercial landings: (a) plot of the 45-yr (1930–74) time series with the linear trend line drawn in; (b) plot of the detrended data (i.e. residuals); (c) Fourier spectrum of the residuals; and (d) maximum entropy spectrum of the residuals.

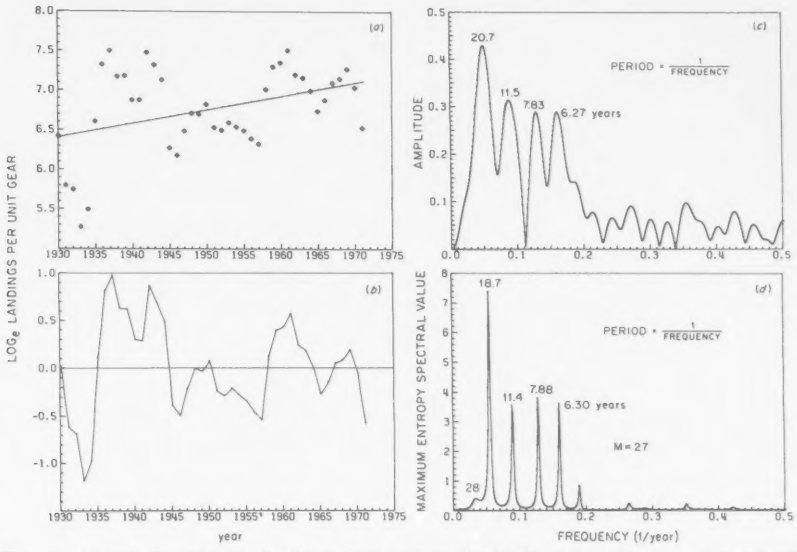

FIG. 5. Results for Maryland striped bass commercial landings per unit gear: (a) plot of the 42-yr (1930–71) time series with the linear trend line drawn in; (b) plot of the detrended data (i.e. residuals); (c) Fourier spectrum of the residuals; and (d) maximum entropy spectrum of the residuals.

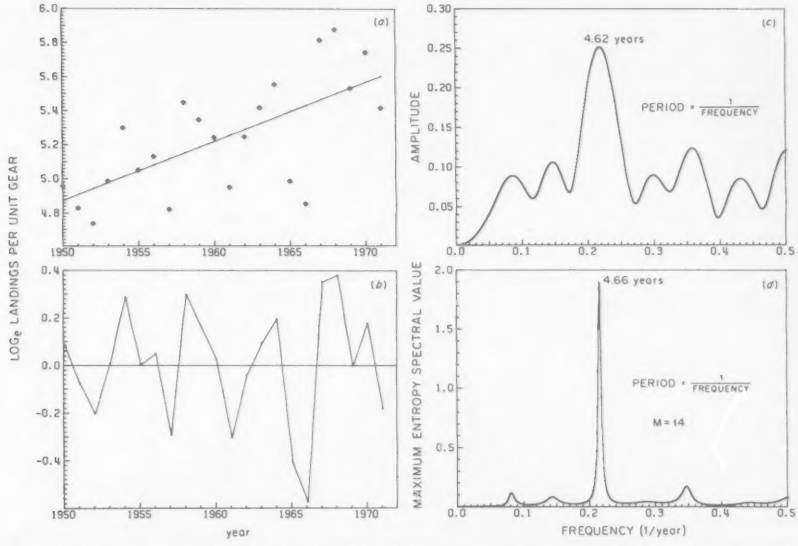

FIG. 6. Results for North Carolina striped bass commercial landings per unit gear: (a) plot of the 22-yr (1950–71) time series with the linear trend line drawn in; (b) plot of the detrended data (i.e. residuals); (c) Fourier spectrum of the residuals; and (d) maximum entropy spectrum of the residuals.

entropy spectra. The slope of the regression line for LG (Fig. 5a) is significantly less ($P < 0.01$) than for L (Fig. 4a), which suggests that part of the long-term increase in striped bass L in Maryland is associated with gear effects rather than an actual increase in the size of the striped bass population. The detrended time series are similar, the major difference being that values for 1947–55 are generally below the mean (0.0 after

detrending) for LG (Fig. 5b) and above the mean for L (Fig. 4b). The number, position, and relative power of the peaks in the maximum entropy spectrum as compared to the Fourier spectrum are very similar for the L time series (Fig. 4c and 4d) and for the LG time series (Fig. 5c and 5d), although once again the sharper resolution obtained with MESA is evident. The main difference between the L and L/G spectra is that the peak in the L spectrum at 44 yr (Fig. 4) appears at 28 yr in the L/G spectrum (Fig. 5).

North Carolina

The North Carolina maximum entropy spectrum (Fig. 3 and 6) is appreciably different from all the other spectra (Fig. 3), a finding that is also suggested by the autocorrelation analysis (Table 2). There is relatively little structure in the North Carolina spectrum, especially when compared with the Maryland spectra (Fig. 4–5). The single statistically significant peak is at about 5 yr. That the structure of the North Carolina time series is somewhat unique is consistent with evidence indicating that there is a discrete North Carolina striped bass stock that spawns in the Roanoke River and that does not mix with Chesapeake and Hudson stocks to any appreciable extent (Raney and deSylva 1953; TI 1976; Vladykov and Wallace 1952). To the extent that the periodicities in any of these time series are causually related to environmental factors, the North Carolina results suggest (1) that the relative importance of these environmental factors in enhancing survival of the young may differ in the Roanoke as compared with the Chesapeake or Hudson, and (2) that the fluctuations in these environmental factors may differ in the Roanoke as compared with the Chesapeake or Hudson.

Conclusion

Assuming that commercial fisheries data provide an indirect, though reasonable, measure of the occurrence of dominant year-classes, even for multi-age-class spawners such as striped bass, the results of our autocorrelation analyses and spectral analyses do not support the hypothesis of a pronounced or simple cycle of 6 yr or any other time interval in the appearance of dominant year-classes in Atlantic Coast striped bass populations. Thus, we conclude that impact assessments and monitoring programs should not be predicated on the expectation of such cycles. Extensive but unpredictable variability in striped bass year-class strength seems to be inevitable, and this variability will continue to frustrate individuals involved in managing and attempting to assess the effects of power plants and other sources of man-induced mortality on these stocks.

ABLES, J. G. 1974. Maximum entropy spectral analysis. Astron. Astrophys. Suppl. 15: 383–393.

BOX, G. E. P., AND G. M. JENKINS. 1970. Time series analysis. Holden-Day, San Francisco, Calif. 553 p.

BULMER, M. G. 1974. A statistical analysis of the 10-year cycle in Canada. J. Anim. Ecol. 43: 701–718.

BURG, J. P. 1975. Maximum entropy spectral analysis. Ph.D. Dissertation, Stanford Univ., Stanford, Calif. 123 p.

ELTON, C., AND M. NICHOLSON. 1942. The ten-year cycle in numbers of the lynx in Canada. J. Anim. Ecol. 11: 215–244.

FINERTY, J. 1972. Cyclic fluctuations in biological systems: a revaluation. Ph.D. Dissertation, Yale Univ., New Haven, Conn. 189 p.

FULLER, W. A. 1976. Introduction to statistical time series. John Wiley & Sons, New York, N.Y. 470 p.

JENKINS, G. M., AND D. G. WATTS. 1968. Spectral analysis and its applications. Holden-Day, San Francisco, Calif. 525 p.

KENDALL, M. G. 1973. Time series. Charles Griffin and Company Limited, London. 197 p.

KIRK, B. L., B. W. RUST, AND W. VAN WINKLE. 1979. Time series analysis by the maximum entropy method. Oak Ridge National Laboratory, Oak Ridge, Tenn. ORNL-5332. (In press)

KOO, T. S. Y. 1970. The striped bass fishery in the Atlantic states. Chesapeake Sci. 11: 73–93.

MANSUETI, R. J. 1961. Age, growth, and movements of the striped bass, *Roccus saxatilis*, taken in size selective fishing gear in Maryland. Chesapeake Sci. 2: 9–36.

MCHUGH, J. L. 1972. Marine fisheries of New York State. Fish. Bull. 70: 585–610.

MORAN, P. A. P. 1949. The statistical analysis of the sunspot and lynx cycles. J. Anim. Ecol. 18: 115–116.

1953. The statistical analysis of the Canadian lynx cycle. I. Structure and prediction. Aust. J. Zool. 1: 163–173.

PLATT, T., AND K. L. DENMAN. 1975. Spectral analysis in ecology, p. 189–210. *In* R. F. Johnston et al. [ed.]. Annual review of ecology and systematics. Annual Reviews Inc., Palo Alto, Calif.

RANEY, E. C., AND D. D. DESYLVA. 1953. Racial investigations of the striped bass, *Roccus saxatilis* (Walbaum). J. Wildl. Manage. 17: 495–509.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

RUST, B. W., B. S. LUGUE, AND W. VAN WINKLE. 1976. Applications of maximum entropy spectral analysis to ecological time series. Bull. Ecol. Soc. Am. 57(1): 36 (Abstr.)

TI (TEXAS INSTRUMENTS, INC.). 1976. Report on relative contribution of Hudson River striped bass to the Atlantic Coastal fishery. Prepared for Consolidated Edison Company of New York, Inc., New York, N.Y. (December 1976).

ULRYCH, T. J. 1975. Maximum entropy spectral analysis and autoregressive decomposition. Rev. Geophys. Space Phys. 13: 183–200.

USNRC (U.S. NUCLEAR REGULATORY COMMISSION). 1975. Final environmental statement related to operation of Indian Point Nuclear Generating Plant, Unit No. 3. Consolidated Edison Company of New York, Inc. Docket No. 50-286, 2 vol. (February 1975).

VLADYKOV, D. V. D., AND D. H. WALLACE. 1952. Studies of the striped bass, *Roccus saxatilis* (Walbaum), with special reference to the Chesapeake Bay region during 1936–1938. Bull. Bingham Oceanogr. Coll. 14: 132–177.

WILLIAMSON, M. 1972. The analysis of biological populations. Crane, Russak & Company, Inc., New York, N.Y. 180 p.

Modification of the Rheotropic Behavior of Male Rainbow Trout (*Salmo gairdneri*) by Ovarian Fluid

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EMANUEL, M. E., AND J. J. DODSON. 1979. Modification of the rheotropic behavior of male rainbow trout (*Salmo gairdneri*) by ovarian fluid. J. Fish. Res. Board Can. 36: 63–68.

The upstream orientation and frequency of upstream movement of ripe male rainbow trout (*Salmo gairdneri*) in the presence of ovarian fluid obtained from spawning females of the same species were observed and quantified. In a stream tank, male trout moved upstream in the ovarian fluid odor plume. In an optomotor tank, male trout exhibited an increase in the frequency of upstream orientation and movement in the presence of diffuse, nondirectional ovarian fluid. It is concluded that water currents provide directional cues and olfactory stimuli regulate the orientational and kinetic components of the rheotropic response. The significance of this mechanism of orientation in fish migration is discussed.

Key words: rheotropism, behavior, olfaction, orientation, migration, ovarian fluid

EMANUEL, M. E., AND J. J. DODSON. 1979. Modification of the rheotropic behavior of male rainbow trout (*Salmo gairdneri*) by ovarian fluid. J. Fish. Res. Board Can. 36: 63–68.

Nous avons observé et quantifié l'orientation vers l'amont et la fréquence des mouvements vers l'amont de truites arc-en-ciel mâles matures en présence de liquide ovarien de femelles de la même espèce en voie de fraie. Dans un bassin dans un cours d'eau, les truites mâles se dirigent vers l'amont dans la zone d'odeur du liquide ovarien. Dans un bassin optomoteur, les truites mâles accusent une augmentation de fréquence de l'orientation des mouvements vers l'amont en présence de liquide ovarien diffus, non directionnel. Nous concluons que les courants d'eau fournissent des indications quand à la direction et que les stimuli olfactifs règlent la partie orientation et cinétique de la réaction rhéotropique. Nous analysons la signification de ce mécanisme d'orientation chez les poissons.

Received July 24, 1978
Accepted October 27, 1978

Reçu le 24 juillet 1978
Accepté le 27 octobre 1978

THE term rheotropism describes all the reactions that a fish might make in response to a current of water, either directly as a response to water flowing over the body surface or indirectly as a response to the visual, tactile, or inertial stimuli resulting from the displacement of fish in space (Harden Jones 1968; Arnold 1974). The rheotropic response consists of an orientational and a kinetic component; fish generally orient into a current and adjust their swimming speeds in response to the rate of the current. Several environmental factors affect the orientational and kinetic components of rheotropism and some evidence suggests that such environmental regulation of rheotropism is important in the migration of fish (Dodson and Young 1977).

Olfactory clues have long been implicated in the migration of fish. The olfactory hypothesis for salmon homing (Hasler and Wisby 1951) has been largely verified by a series of experiments using artificial imprinting to a synthetic chemical (Hasler et al. 1978). However, the natural olfactory cues associated with home streams have not been identified. Hasler and Wisby (1951) postulated that each stream has a different odor due to local differences in soil and vegetation of the drainage basin. Solomon (1973) postulated that metabolic products or race-specific pheromones may be responsible for the homing of Atlantic salmon, and Nordeng (1977) presented a similar hypothesis for migratory Arctic char (*Salvelinus alpinus*). The mechanism(s) of orientation by which fish obtain directional information from such olfactory cues has not been adequately demonstrated.

The behavior of mature male fish is altered by a pheromone associated with the gravid female (Tavolga 1956; Timms and Kleerekoper 1972; Crapon de

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Printed in Canada (J5315)
Imprimé au Canada (J5315)

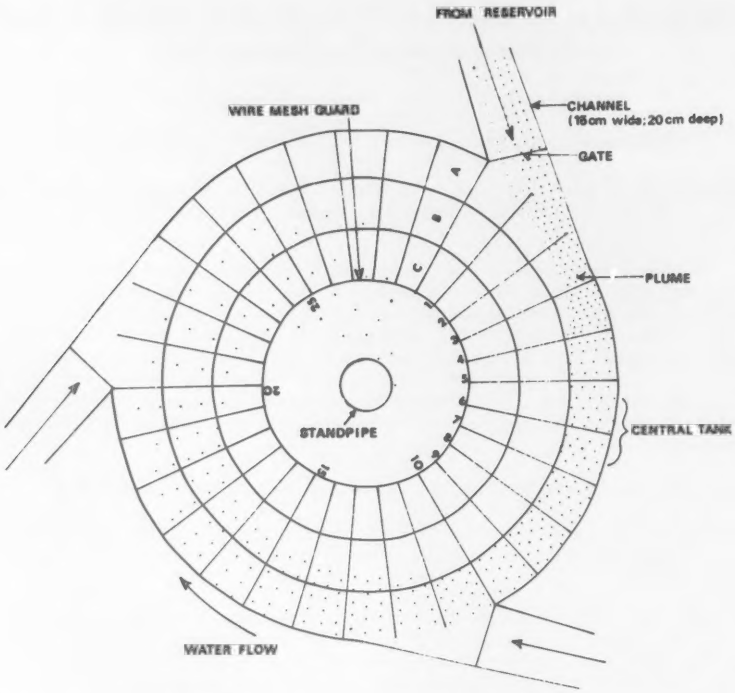

FIG. 1. Circular stream tank used to assess the attractiveness of ovarian fluid to male rainbow trout. Letters indicate the 3 radial sections and numbers indicate the 30 angular sections. Stippling indicates the extent and concentration gradient of the odor plume. Supply reservoirs are omitted from the diagram.

Caprona 1974; Partridge et al. 1976), and ovarian fluid contains this as yet unidentified pheromone (Newcombe and Hartman 1973; Partridge et al. 1976). In this study, the rheotropic response of ripe male rainbow trout to a real and simulated water current in the presence of dilute ovarian fluid obtained from spawning females was observed. The purpose of the study was to determine whether ovarian fluid would stimulate the upstream movement of male trout and to describe the mechanism(s) of orientation responsible for any such movement.

Materials and Methods

In the fall of 1976 ripe male rainbow trout (*Salmo gairdneri*) were obtained from Creekbank Hatchery, Elmira, Ontario, and held in the laboratory in 790-L and 2500-L tanks equipped with fluorescent cool white lighting and time switches set for an 8 h daylength. The tanks were supplied with local well water at a constant temperature of 11°C. The trout were 30–50 cm long (FL) and weighed 200–400 g.

The rheotropic behavior of rainbow trout in the presence of ovarian fluid was observed initially in a circular stream tank (Fig. 1) made of galvanized steel and consisting of three channels 60 cm long attached tangentially to a central tank 152 cm diam and 23 cm deep. Each channel was attached distally to an 80-L supply reservoir and water from the reservoirs flowed down the channels into the central tank at 15 cm/s. The water level was maintained at 18 cm by an adjustable standpipe located in the middle of the central tank. A wire mesh guard 60 cm diam was placed around the standpipe to prevent fish from being sucked down the outlet. Wire mesh gates were placed at the entrance of each channel to the central tank. Therefore, fish were restricted in their movements to a circular channel 46 cm wide. Black curtains surrounded the stream tank which was illuminated from 6 m above by a 7500-W spotlight. All observations were recorded with an XL-400 Minolta Super 8 movie camera at a rate of 1 exposure per minute from the same height.

Groups of five fish each were observed swimming in the stream tank. Each group was allowed 30 min to acclimate following their introduction into the tank. After a 30-min observational period during which time fish movement was filmed, ovarian fluid was introduced at a constant rate into one of the channels and fish movement filmed for another 30 min. The source channel was changed for successive replicates.

Ovarian fluid was collected on several occasions from female rainbow trout being stripped of their eggs during the hatchery spawning period. The fluid as collected was considered to be a 100% solution and subsequent dilutions were made by mixing the ovarian fluid with well water.

Preliminary testing at concentrations of 50, 10, 1, 0.5, 0.1, and 0.01 μL/L in the source channel indicated that obvious changes in rheotropic behavior occurred at the 0.1-μL/L level. Therefore, 15 replicates of five fish each were observed in the stream tank in response to ovarian fluid at a concentration of 0.1 μL/L in the source channel.

To analyze the movement of ripe male trout in response to ovarian fluid, the stream tank was divided into 3 radial (designated A, B, C) and 30 angular positions (designated 1, 2, 3 . . ., 30) relative to the source channel, thus splitting the central tank into 90 sections (Fig. 1). The films of fish movement were viewed on an editing scope and each fish was placed into one section for each minute of observation. Dye was introduced into each channel on several different occasions and the resultant plume was plotted (Fig. 1). The plume initially moved downstream close to the outer wall of the tank (sections A1–A14) before spreading out and moving toward the center of the tank (sections B11–B23 and C16–C26). The numbers of fish observations before and after the introduction of ovarian fluid were recorded for the upstream end of the plume (defined as sections A1–A14) where the concentration of ovarian fluid was greatest and for the downstream end of the plume (defined as sections B11–B23 and C16–C26) where the concentration declined. Variations occurred in the extent of the plume due to uncontrolled fluctuations in water velocity and minor differences in the geography of the tank between different channels. As it was impossible to monitor the exact position of the plume during each replicate, the plume as defined above represents its minimum extent. Thus we have tended to underestimate the extent of the plume and, as a result, the number of observations of fish in the plume.

The data for the number of observations of fish in the plume before and after the addition of ovarian fluid was analyzed by a 2 factor analysis of variance with interaction and replication. The model was of the form

$$Y_{ijk} = \mu + t_i + p_j + (tp)_{ij} + \gamma_k + \epsilon_{ijk}$$

where μ is the overall mean
t_i is the effect of the ith time interval
$i = 1, 2$ (before, after)
p_j is the effect of the jth plume segment
$j = 1, 2$ (upstream, downstream)
$(tp)_{ij}$ is the time interval $\times$ plume segment interaction
γ_k is the effect of the kth replicate
Y_{ijk} is the number of observations of fish for the kth replicate at the ith time interval in the jth plume segment
ϵ_{ijk} is the experimental error corresponding to Y_{ijk}.

Observations in the stream tank alone did not adequately describe the mechanism of orientation responsible for the movement of male trout responding to ovarian fluid. To investigate this mechanism further, the rheotropic response of ripe male trout in the presence of ovarian fluid was measured in the optomotor tank described and illustrated by Dodson and Young (1977). The optomotor tank did not generate a true current but rather simulated the visual stimuli produced by displacement in a water current by moving a striped background past the fish. Therefore, unlike the stream tank, the ovarian fluid in the optomotor tank was diffuse and nondirectional thus eliminating the odor gradient as an orientational cue.

The rheotropic response consists of an orientational and kinetic component. The orientational component was quantified by recording the proportion of total observation time that fish spent swimming in the same direction as the moving background (frequency of positive rheotaxis) which is equivalent to orienting upstream. The kinetic component of the rheotropic response was quantified by recording the proportion of total observation time that the fish spent swimming faster than the moving background (frequency of gain) which is equivalent to upstream displacement.

Five groups of 10 ripe male rainbow trout each were observed singly in the optomotor tank in the presence of ovarian fluid at concentrations of 0.0 (control), 10^{-4}, 10^{-3}, 10^{-2}, and 10^{-1} μL/L and the frequency of positive rheotaxis and gain were recorded for each. Observations were made for 15 min following an acclimation period of 5 min with the background revolving at a rate equivalent to a water current of 15 cm/s. These levels were chosen as indicative of the ovarian fluid concentration in the stream tank plume where the 10^{-1} μL/L solution in the source channel was rapidly diluted upon entry into the central tank.

The data for frequency of positive rheotaxis and frequency of gain were analyzed using simple one-way analyses of variance. Since treatments (ovarian fluid concentration) were qualitatively similar and balanced ($n = 10$ for all treatments), the experimental error (s^2) for each analysis of variance was used to generate the Least Significant Difference (LSD) at the 5% probability level for each of the two behavioral parameters. The means for each treatment were plotted with their appropriate LSD for frequency of positive rheotaxis and frequency of gain to illustrate any differences between the treatment means.

Results

Stream Tank Observations

In the absence of any odorous cues, mature male rainbow trout were observed to swim continuously in the stream tank both upstream and downstream. Agonistic behavior was prevalent with much displaying, circling, and tail-nipping occurring. On addition of the ovarian fluid, a marked decline in agonistic behavior was observed. The orientation of the fish became predominantly upstream as most male trout were observed to move to the outer periphery of the stream tank and upstream into the area of the plume emanating from the source channel. Although one or two trout in some replicates tended to stem the current and remain within the plume, most continued to swim either around the tank and back up the plume along the outer periphery of the tank or in zig-zag fashion across the stream tank in and out of the upstream end of the odor plume. This behavior continued for the entire 30 min that ovarian fluid was present in the tank.

The analysis of the films confirmed quantitatively the behavior described qualitatively above. The total number of observations of 75 fish (15 replicates $\times$ 5 fish) in the upstream segment of the odor plume (sections A1–A14) and in the downstream segment of the odor plume (sections B11–B23 and C16–C26) before and after addition of ovarian fluid were as follows:

	Upstream	Downstream
Before	364	523
After	472	424

The analysis of variance revealed that although the number of observations of fish in the entire plume did not differ significantly between the 30-min time intervals before and after the addition of ovarian fluid, the interaction between time interval and plume segment was significant ($F_{1/42} = 5.12$; $0.01 < P < 0.05$). Therefore, fish observed in the area of the plume spent significantly more of their time in the upstream segment of the plume after the addition of ovarian fluid. No significant variation occurred between replicates ($F_{14/42} = 1.21$; $P > 0.05$).

Optomotor Tank Observations

Variation in the frequency of positive rheotaxis was not significant ($F = 1.5$; $P > 0.05$; $s^2 = 0.065$; $n = 50$) and, therefore, the use of the LSD to detect differences between mean frequencies of positive rheotaxis must be interpreted with caution. However, there is a trend (Fig. 2A) in which the frequency of positive rheotaxis increased to a maximum at an ovarian fluid concentration of 10^{-3} μL/L and then declined at higher concentrations. The frequency of positive rheotaxis at the 10^{-3} μL/L treatment level was significantly greater than that observed at the control, 10^{-1} and 10^{-4} μL/L treatment levels (Fig. 2A).

Variation in the frequency of gain of male trout in the presence of ovarian fluid was significant ($F = 2.5$; $P = 0.05$; $s^2 = 0.074$; $n = 50$). As with frequency of positive rheotaxis, the maximum frequency of gain occurred at an ovarian fluid concentration of 10^{-3} μL/L. The frequency of gain at the 10^{-3} μL/L treatment level was significantly greater than that observed at all other treatment levels (Fig. 2B).

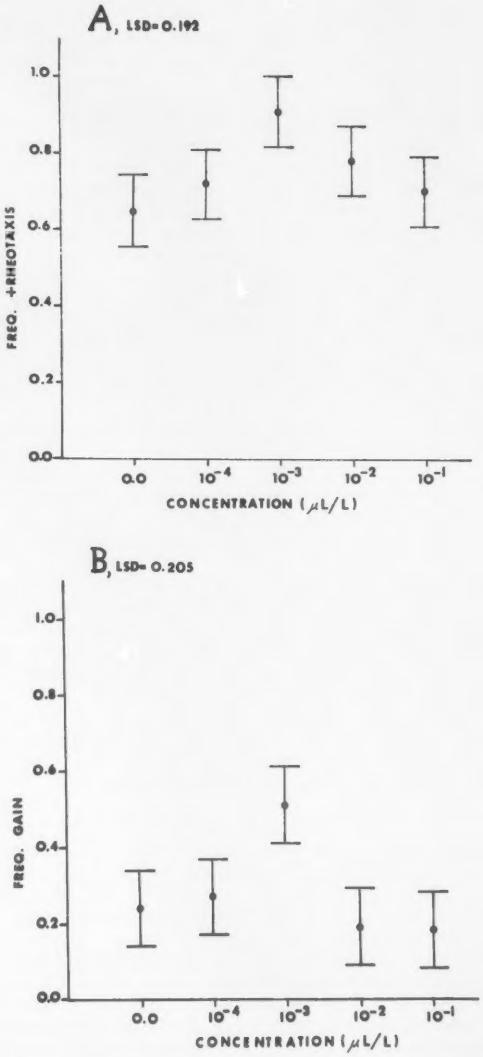

FIG. 2. Effect of dilute ovarian fluid on the frequency of positive rheotaxis (A) and the frequency of gain (B) of mature male rainbow trout. Each point on the graphs represents the mean of 10 fish. Bars across the points indicate the Least Significant Difference (LSD) as calculated from the analysis of variance of each behavioral parameter. Overlapping bars indicate no significant difference between means at the 5% probability level.

Discussion

This study has shown that the rheotropic response of ripe male rainbow trout is affected by dilute ovarian fluid obtained from spawning female rainbow trout. In the circular stream tank, male trout moved upstream in the plume created by ovarian fluid emanating from a source channel. In the optomotor tank, male trout showed an increase in the frequency of upstream orientation and, more significantly, in the frequency of upstream movement in the presence of diffuse, nondirectional ovarian fluid at concentrations equivalent to those existing in the plume of the stream tank. These observations demonstrate that the response of trout observed in the stream tank was not solely due to the presence of an odor gradient. Rather, the mechanism of orientation as revealed in the optomotor tank is related to the regulation of rheotropism, whereby the ovarian fluid acts as a sign stimulus regulating the orientational and kinetic components of the response to the water current. A fish using such a mechanism can respond unidirectionally to an attractant odor in a water current when no concentration gradient exists. This would be particularly important to a migrating fish far from its goal, where olfactory cues indicative of home may be present but no concentration gradient would exist due to the dilution and dispersion of such cues far from their source.

The majority of male trout observed in the circular

stream tank spent much of their time moving in and out of the odor plume during the period ovarian fluid was present in the tank. This may have represented some kind of gradient or boundary response and suggests that trout are capable of using an odor gradient when present. Another consequence of such behavior was that few trout were exposed constantly to the odor. This may have contributed to preventing the adaptation of the olfactory sense to ovarian fluid over the 30-min observation period.

The optomotor tank observations show a trend in which the frequency of positive rheotaxis and gain is at a maximum in the presence of 10^{-3} μL/L ovarian fluid and decreases at greater or lesser concentrations. Thus it appears that a maximum response occurs at a particular concentration of the odor. A similar situation was reported by Timms and Kleerekoper (1972) from a study of the locomotor movement of ripe male channel catfish (*Ictalurus punctatus*) in response to a sexual pheromone released by a ripe female. They noted that at an appropriate strength of the stimulus the response was a well-defined tropotaxis (simultaneous comparison of the stimulus by lateral receptors) and that when presented with a choice between two concentrations of the pheromone, the catfish were not attracted preferentially to the stronger source. Possibly lower concentrations of the pheromone serve as guides leading receptive males to the spawning areas.

No significant changes occurred in the rheotropic response of rainbow trout at the highest concentration of ovarian fluid (10^{-1} μL/L) tested in the optomotor tank. As ovarian fluid plays an important role in sexual behavior (Tavolga 1956; Partridge et al. 1976), the possibility exists that at higher concentrations of ovarian fluid, receptive males may require other cues, such as visual or tactile contact with females, to release the next sequence of behavioral responses. Kleerekoper (1972) has suggested that the same sign stimulus may elicit variable responses in the presence of different cues. Hence in the presence of increasingly higher concentrations of ovarian fluid, the absence of other cues associated with females and spawning may have caused an inhibition of the upstream movement of receptive males. In nature, such a mechanism would prevent males from overshooting nearby spawning grounds where ovarian fluid concentrations would be greatest.

There are many examples in the literature of the attraction of fish by various odorous substances (reviewed for freshwater fish by Solomon 1977). Unfortunately, only a few of these studies have attempted to determine the mechanism of orientation responsible for the observed movement. Mathewson and Hodgson (1972) observed that the lemon shark (*Negaprion brevirostris*) on encountering an olfactory stimulus would swim upstream into the strongest current even when the source of the attractant was placed in the weakest current of an experimental enclosure. They concluded that the attractant odor triggered a positive rheotropic response with the stronger current providing better orientational cues than weaker currents. Kleerekoper (1967) suggested that an attractant odor released rheotactic responses in several marine and freshwater species observed in an experimental tank, so that the localization of the odor source took place through rheotaxis rather than through orienting cues provided by the odor gradient. Kleerekoper et al. (1975) demonstrated that the nurse shark (*Ginglymostoma cirratum*) required flowing water as a direction vector for the precise localization of the source of an attractant chemical stimulus.

Several investigations into the mechanisms of fish migration have demonstrated mechanisms of orientation involving the modification of rheotropism by olfactory sign stimuli. Creutzberg (1961) demonstrated that the rheotropic response of elvers (*Anguilla anguilla*) changed in response to the tide. On ebb tide the elvers swam against the current whereas on flood tide they rose from the bottom and either swam with or were carried passively by the current, this change in behavior being stimulated by an unidentified chemical characteristic of inland water. Miles (1968) observed a similar rheotropic response to freshwater by elvers of *Anguilla rostrata*. Dodson and Leggett (1973) observed that adult American shad (*Alosa sapidissima*) homing to the Connecticut River from Long Island Sound exhibited different rheotropic responses to ebb and flood tide which resulted in unidirectional displacement, and subsequently demonstrated (1974) this to be dependent on the presence of olfactory cues acting as sign stimuli. Scholz et al. (1972) observed that migrating adult chum (*Oncorhynchus keta*) and coho (*O. kisutch*) salmon responded differently to ebb and flood currents and hypothesized that olfactory mechanisms were responsible for their observations. Atlantic salmon (*Salmo salar*, Stasko et al. 1973a) and pink salmon (*Oncorhynchus gorbuscha*, Stasko et al. 1973b) also exhibit different rheotropic responses to ebb and flood tide currents during their homeward migrations but the mechanism(s) responsible for this behavior has not been described.

In conclusion, this study has demonstrated that dilute ovarian fluid stimulates the upstream movement of ripe male trout. This would likely be of orientational significance only later in the migration after spawning had begun. The olfactory cue(s) responsible for the uniqueness and attractiveness of the natal stream is no doubt a complex of chemical characteristics whose nature remains unclear. Finally, this study has demonstrated that trout can respond unidirectionally to an attractant odor in a water current when no concentration gradient exists. This mechanism of orientation involves water currents providing the directional cues and the olfactory stimuli regulating the rheotropic response.

Acknowledgments

We acknowledge the valuable assistance of Dr J. C. Young

and the University of Waterloo Statistical Consulting Service in the preparation of this manuscript. This project was partially funded by an NRC operating grant to J.J.D.

ARNOLD, G. P. 1974. Rheotropism in fishes. Biol. Rev. 49: 515–576.

CRAPON DE CAPRONA, M. D. 1974. The effect of chemical stimuli from conspecifics on the behavior of *Haplochromis burtoni* (Cichlidae, Pisces). Experientia 30: 1394–1395.

CREUTZBERG, F. 1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in a tidal area. Neth. J. Sea Res. 1: 257–338.

DODSON, J. J., AND W. C. LEGGETT. 1973 Behavior of adult American shad (*Alosa sapidissima*) homing to the Connecticut River from Long Island Sound. J. Fish. Res. Board Can. 30: 1847–1860.

1974. Role of olfaction and vision in behavior of American shad (*Alosa sapidissima*) homing to the Connecticut River from Long Island Sound. J. Fish. Res. Board Can. 31: 1607–1619.

DODSON, J. J., AND J. C. YOUNG. 1977. Temperature and photoperiod regulation of rheotropic behavior in prespawning common shiners, *Notropis cornutus* (Mitchill). J. Fish. Res. Board Can. 34: 341–346.

HARDEN JONES, F. R. 1968. Fish migration. St. Martin's Press, New York, N.Y. 325 p.

HASLER, A. D., A. T. SCHOLZ, AND R. M. HORRALL. 1978. Olfactory imprinting and homing in salmon. Am. Sci. 66: 347–355.

HASLER, A. D., AND W. J. WISBY. 1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. Am. Nat. 85: 223–238.

KLEEREKOPER, H. 1967. Some aspects of olfaction in fishes, with special reference to orientation. Am. Zool. 7: 385–395.

1972. Orientation through chemo-reception in fishes. *In* S. R. Galler et al. [ed.] Animal Orientation and Navigation. A symposium held at Wallops Station, Virginia, 1970. Scientific and Technical Information Office, NASA, Washington, D.C.

KLEEREKOPER, H., D. GRUBER, AND J. MATIS. 1975. Accuracy of localization of a chemical stimulus in flowing and stagnant water by the nurse shark (*Ginglymostoma cirratum*). J. Comp. Physiol. 98: 257–275.

MATHEWSON, R. F., AND E. S. HODGSON. 1972. Klinotaxis and rheotaxis in orientation of sharks toward chemical stimuli. Comp. Biochem. Physiol. 42A: 79–84.

MILES, S. G. 1968. Rheotaxis of elvers of the American eel, *Anguilla rostrata*, in the laboratory to water from different streams in Nova Scotia. J. Fish. Res. Board Can. 21: 1591–1602.

NEWCOMBE, C., AND G. HARTMAN. 1973. Some chemical signals in the spawning behavior of rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 30: 995–997.

NORDENG, H. 1977. A pheromone hypothesis for homeward migration in anadromous salmonids. Oikos 28: 155–159.

PARTRIDGE, B. L., N. R. LILEY, AND N. E. STACEY. 1976. The role of pheromones on the sexual behavior of the goldfish. Anim. Behav. 24: 291–299.

SCHOLZ, A., D. M. MADISON, A. B. STASKO, R. M. HORRALL, AND A. D. HASLER. 1972. Orientation of salmon in response to currents in or near the home stream. Amer. Zool. 12(4): 654 p.

SOLOMON, D. J. 1973. Evidence for pheromone-influenced homing by migrating Atlantic salmon (*Salmo salar* L.). Nature, Lond. 244: 231–233.

1977. A review of chemical communication in freshwater fish. J. Fish Biol. 11: 363–376.

STASKO, A. B., A. M. SUTTERLIN, S. A. ROMMEL JR., AND P. F. ELSON. 1973a. Migration-orientation of Atlantic salmon (*Salmo salar* L.). Int. Atl. Salmon Symp. 1972, Int. Atl. Salmon Found., Spec. Publ. 4(1): 119–137.

STASKO, A. B., R. M. HORRALL, A. D. HASLER, AND D. STASKO. 1973b. Coastal movements of mature Fraser River pink salmon (*Oncorhynchus gorbuscha*) as revealed by ultrasonic tracking. J. Fish. Res. Board Can. 30: 1309–1316.

TAVOLGA, W. N. 1956. Pre-spawning behavior in the Gobiid fish, *Bathygobius soporator*. Behaviour 9: 53–75.

TIMMS, A. M., AND H. KLEEREKOPER. 1972. The locomotor responses of male *Ictalurus punctatus*, the channel catfish, to a pheromone released by the ripe female of the species. Trans. Am. Fish. Soc. 101: 302–310.

Meristic Variation of *Lycodapus mandibularis* (Pisces: Zoarcidae) and Oceanic Upwelling on the West Coast of North America

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PEDEN, A. E. 1979. Meristic variation of *Lycodapus mandibularis* (Pisces: Zoarcidae) and oceanic upwelling on the west coast of North America. J. Fish. Res. Board Can. 36: 69–76.

Total vertebral counts of *Lycodapus mandibularis* populations in Georgia Strait, British Columbia, are significantly lower than those of southern populations off Oregon and California. The highest temperatures and lowest salinities at 200 m or deeper, where the species is most abundant, are also in Georgia Strait and correlate with the lowest counts. The Strait's deep water originates from tidal mixing of intermediate and estuarine surface waters of lower salinities and higher temperatures, whereas the mechanism in southern latitudes, which instead provides unmixed cooler and saline deep waters, is oceanic upwelling. It is suggested that differences in environment associated with different degrees of upwelling and mixing may cause the lower counts in the Strait of Georgia.

Key words: Lycodapus mandibularis, Zoarcidae, meristic variation, inlets, upwelling, temperature, salinity, northeast Pacific Ocean, zoogeography

PEDEN, A. E. 1979. Meristic variation of *Lycodapus mandibularis* (Pisces: Zoarcidae) and oceanic upwelling on the west coast of North America. J. Fish. Res. Board Can. 36: 69–76.

Le nombre total des vertèbres chez les populations de *Lycodapus mandibularis* du détroit de Georgie, en Colombie-Britannique, est nettement inférieur à celui des populations méridionales du large de l'Orégon et de la Californie. Les températures les plus élevées et les salinités les plus faibles à 200 m et plus, où l'espèce se rencontre en plus grande abondance, se trouvent également dans le détroit de Georgie et s'accordent avec les nombres les plus bas. Les eaux profondes du détroit tirent leur origine du mélange par la marée des eaux superficielles intermédiaires et estuariennes de faibles salinités et de températures élevées, alors qu'aux latitudes méridionales, le mécanisme qui, au lieu de cela, fournit des eaux profondes non mélangées, plus froides et plus salées, est une remontée des eaux profondes. Nous suggérons que les différences dans l'environnement associées à différents degrés de remontée d'eaux profondes et de mélange peuvent être responsables des nombres vertébraux plus faibles dans le détroit de Georgie.

Received July 25, 1978
Accepted October 27, 1978

Reçu le 25 juillet 1978
Accepté le 27 octobre 1978

VERTEBRAL numbers of fishes are well known to be influenced by environmental as well as genetic factors (Hubbs 1922; Taning 1952; Lindsey 1961; Rosenblatt 1963). As a general rule, fewer vertebrae occur in populations of a species from lower latitudes. A selective response to prevailing higher temperatures during embryonic development probably induces such clines (Jordan 1891; Lindsey 1961; Peden 1966), although some experiments on rearing fish larvae at different temperatures suggest intermediate temperatures may also produce the most extreme counts (Lindsey 1961). Peden and Anderson (1978) found an exception to Jordan's (1891) general observation of lowest counts at low latitudes when they described populations of *Lycodapus mandibularis* from Georgia Strait, British Columbia, with many fewer vertebrae compared to southern samples from off Oregon and California (Fig. 1). In fact, the counts were so divergent that the differences at first suggested two distinct species, until Peden and Anderson's study found geographically and meristically intermediate populations from Puget Sound that indicated *L. mandibularis* was merely a wide ranging polymorphic species. As the species is known from Prince William Sound, Alaska, to La Jolla, California, there is a wide geographic range to test for a latitudinal cline of vertebral counts. This study describes the geographic pattern of vertebral numbers in *L. mandibularis* and discusses some correlated oceanographic features that may explain this pattern.

Materials and Methods

Total numbers of vertebrae were obtained from radiographs and the hypural centrum was counted as the

Printed in Canada (J5319)
Imprimé au Canada (J5319)

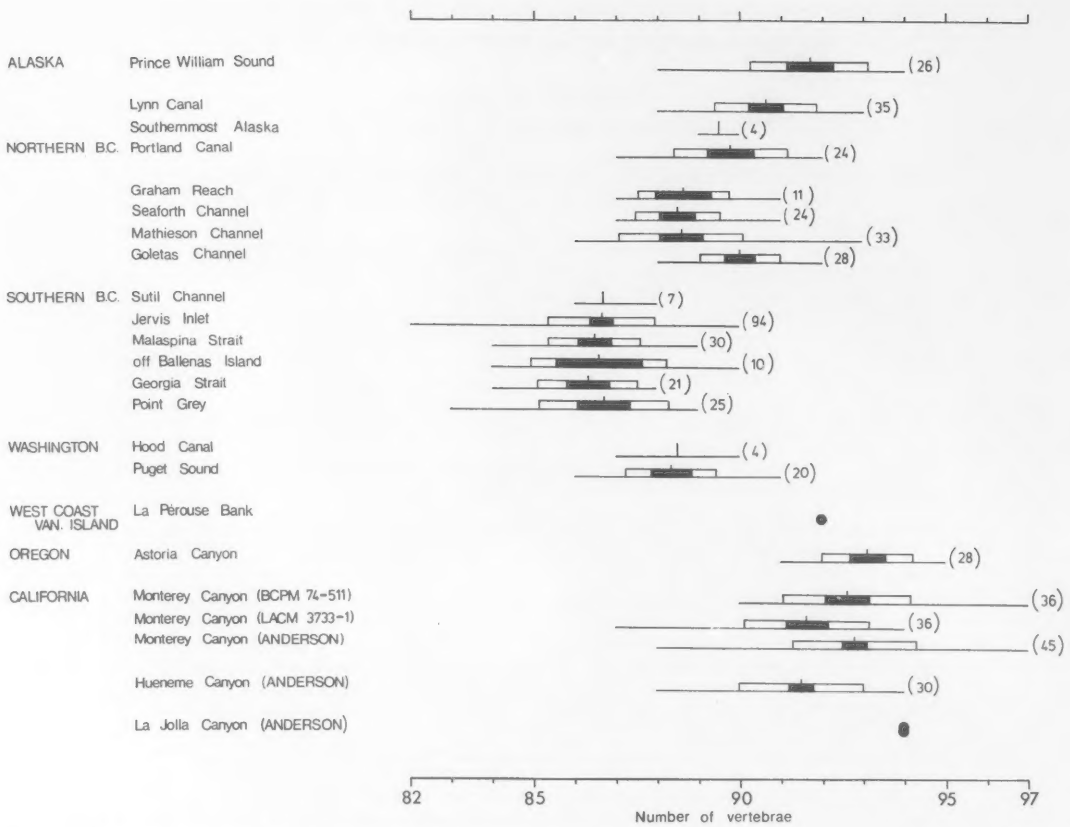

FIG. 1. Range of total numbers of vertebrae in *Lycodapus mandibularis*. Graphs follow method of Hubbs and Hubbs (1953) with the short vertical line indicating mean, dark bar indicating two standard errors on either side of mean, and dark bar plus light bar representing 1 SD on either side of mean. Numbers within parentheses represent sample sizes.

posteriormost vertebra. The total number of collections available for study were listed by Peden and Anderson (1978) but usable radiographs were obtained only from the following localities (Fig. 1): Prince William Sound (collection numbers UA-216, UA-PWS-16, UA-2024, UA-1108, AB 62-503); various localities in southeastern Alaska (AB 62-486, AB 64-84, AB 64-99, AB 65-18); Lynn Canal in S.E. Alaska (AB 65-34, AB 64-1001); northern British Columbia including Portland Canal (BCPM 976-1301), Seaforth Channel (BCPM 976-1293), Mathieson Channel (BCPM 976-1294, BCPM 976-1295), Fitz Hugh Sound (BCPM 976-1291, BCPM 976-1292), and Goletas Channel (BCPM 975-708); waters connected to Georgia Strait, British Columbia, including Sutil Channel (FRB Tow 13), Jervis Inlet (BCPM 967-2, BCPM 967-3), Malaspina Strait (FRB Tow 3), Georgia Strait (BCPM 975-232), and off Point Grey (FRB Tows 18 and 23); Hood Canal (UW 19255) and Puget Sound (UW 19248, UW 19264, UW 19263, UW 19257, plus uncatalogued specimens from off Hat Island and Shilshole) in Washington; La Perouse Bank (AB 67-21) off the western side of Vancouver Island; Astoria Submarine Canyon off Oregon (OSU 760, OSU 610, OSU 759, Acona 6302, Acona 6204, Acona 6209, Yaquina 6504); and Monterey Submarine Canyon, California (BCPM 974-511 and LACM 33733). Other counts for the Hueneme Canyon and La Jolla Canyon area off southern California were taken from Anderson (1977). These major localities are mapped in Fig. 2.

Results

GEOGRAPHIC VARIATION OF VERTEBRAL COUNTS IN *L. mandibularis*

The counts of total vertebrae in *L. mandibularis* ranged between 82 and 97 with population means ranging from about 86.5 in Georgia Strait waters to about 93 in Astoria Canyon (Fig. 1). Most notably, the range of counts did not overlap between these two areas. Populations off Alaska, northern British Columbia, as well as in Puget Sound have nearly intermediate mean counts, and although the available samples off California are somewhat intermediate, they tend to have

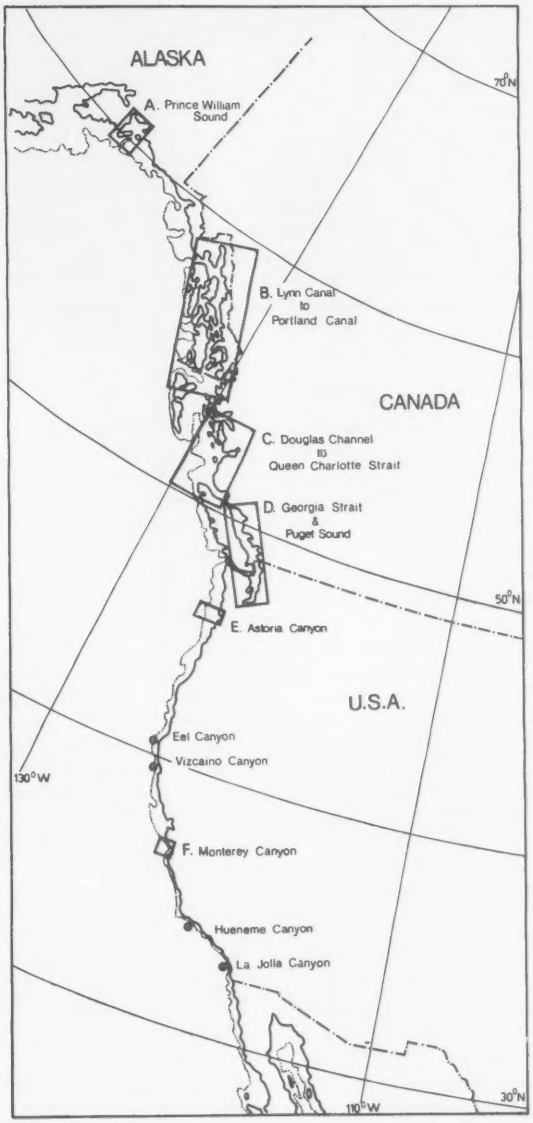

FIG. 2. Sampling areas. Insets indicate areas from which large samples were taken and used in this study. Other sample localities are indicated by black dots.

higher counts than all samples from northern areas.

Dorsal and anal fin ray counts and relative body depth also correlate with vertebral number. However, such relationships should be expected because it is common for fishes of the same species to possess additional fin rays and be relatively more slender when they have more vertebrae — detailed discussion of these particular features would be redundant. Available collections suggest individuals from southern populations off California and Oregon grow to larger sizes than northern *L. mandibularis* (Peden and Anderson 1978), but otherwise, no other features appear to correlate with the geographic pattern of vertebral numbers described here. Some *L. mandibularis* populations are somewhat darker and populations from southern Alaska also tend to have generally fewer vomerine teeth. Because vertebral number demonstrates the most conveniently quantifiable and distinct geographic pattern in the species, it is the principal morphological feature to be discussed in this paper.

Cool water fishes of higher latitudes may be expected to occur in deeper water towards the equator if they are to inhabit waters of similar temperature (Alverson et al. 1964). Unfortunately, available samples of *L. mandibularis* do not permit adequate testing of this premise because the majority of samples were acquired opportunistically as sidelights of other studies. Anderson (1977), whose work off Monterey provides the most meaningful ecological data available to date, found *L. mandibularis* to be concentrated at depths near 500–600 m with diel migration toward shallower depths at night (Fig. 3). Although individuals may infrequently reach surface waters, most *L. mandibularis* are taken in midwaters and few have been taken in bottom trawls (Peden and Anderson 1978). Such midwater habitat is atypical for most zoarcid fishes, and because *L. mandibularis* lacks a swim bladder, the species probably relies on reduced ossification as well as its gelatinous outer body covering to gain buoyancy.

Collections from more northern latitudes appear to be from shallower depths, but the data recorded probably do not accurately indicate the species' preferred depth distribution since most specimens were taken during a standard series of samples from specified oceanographic stations with net hauls taken at only a few specified depths (i.e. 200 m). In addition, one would expect a bias toward shallower samples because smaller vessels with smaller drums of wire make fishing in shallow water more economical, and certainly the deeper waters off the west coast of North America have yet to be extensively sampled for *Lycodapus*.

Of critical importance to environmental control of meristic variation are the prevailing conditions of the habitat in which the fixation of vertebral number occurs during hatching and larval development. Available evidence (Anderson 1977) suggests postlarval depth distribution is similar to that of adults with the smallest postlarvae found throughout the depth range of the species. Eggs, larvae, or postlarvae of zoarcids are generally not found in surface waters as are the planktonic young of many other fish families, but are usually found near the bottom (Mead et al. 1964). Extensive surveys for larval fish in surface layers of Georgia Strait and Saanich Inlet (Barraclough 1967; Barraclough and Fulton 1967, 1968; Barraclough et al. 1968; Robinson

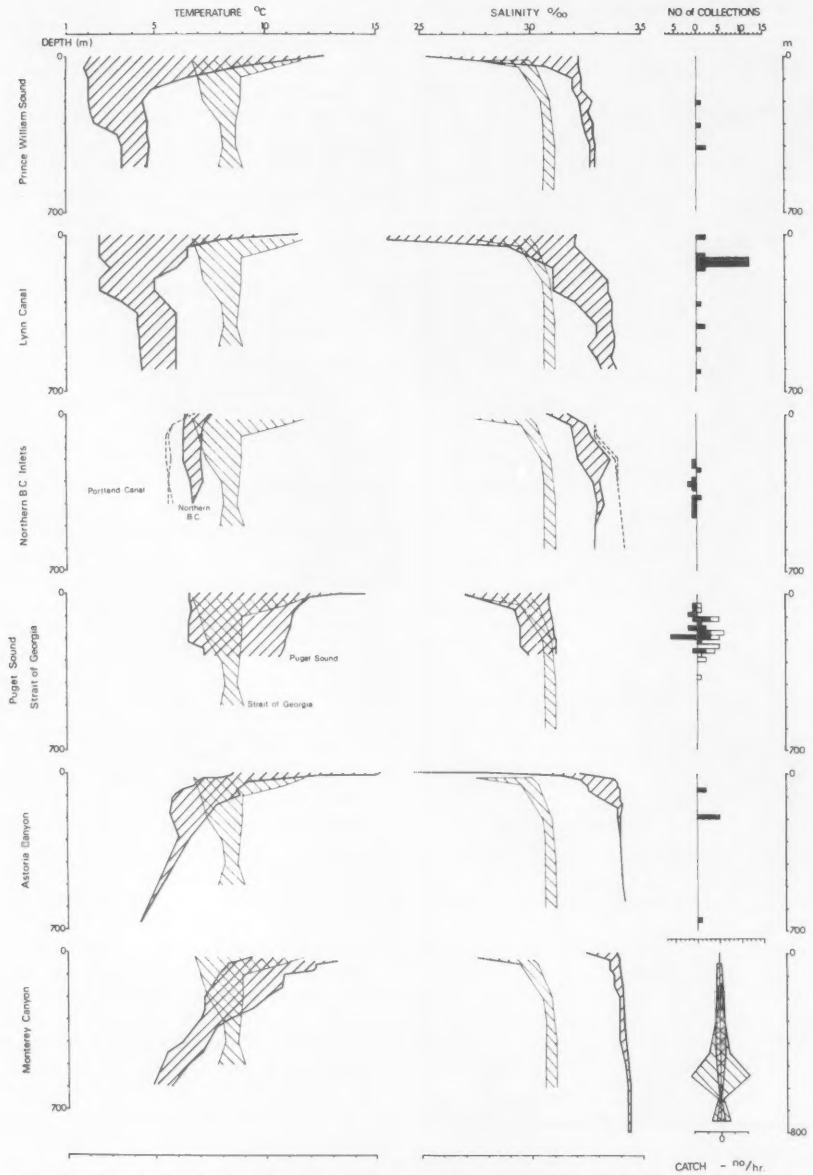

FIG. 3. Depth distribution for ranges of temperatures, salinities, and numbers of samples of *L. mandibularis* observed at localities between Prince William Sound and Monterey. For ease of comparison, observations of salinity and temperature for Georgia Strait are superimposed on each graph. Data taken from following sources: C. M. Schmidt (personal communication) and Muench and Schmidt (1975) for Prince William Sound; Wing (1976) for Lynn Canal; Pickard (1961) for northern British Columbia; Waldichuck (1957) for Georgia Strait; University of Washington (1954) for Puget Sound; Love (1963) for Astoria Canyon; Skogsberg (1936) for Monterey Canyon. Number of collections based on samples observed in this study except that the Monterey record is taken from Anderson (1977). Diel migration is indicated at Monterey by the concentration of specimens at 500–600 m depths during the day and more uniform distribution at night.

et al. 1968a, b) did not yield significant numbers of zoarcid young (only a half dozen reported of unknown identity) even though *L. mandibularis* occurs in substantial numbers throughout the deeper waters of Georgia Strait (Beamish et al. 1976; Peden and Anderson 1978) and such larvae or postlarvae should have been detected if they occurred in the surface layers that were sampled. Peden and Anderson observed *L. mandibularis* as small as 20 mm from deep-water hauls in southeast Alaska and northern British Columbia and M. E. Anderson (personal communication) further observed a 19-mm specimen taken in a closing net at 700 m depths off Monterey suggesting possible development of young in the same deep waters in which adults are found.

Temperature Variation

Because temperature data at point of capture were not available for the majority of museum specimen records, a variety of sources were consulted for the respective waters inhabited by *L. mandibularis* (see Fig. 3). Temperatures were plotted for Prince William Sound, Lynn Canal, northern British Columbia, Puget Sound, Astoria Canyon, as well as Monterey Canyon and compared with temperatures of Georgia Strait. For Prince William Sound, extreme ranges of temperature per depth interval (C. M. Schmidt, Institute of Marine Sciences, University of Alaska unpublished data; and Muench and Schmidt 1975) indicate water temperatures of 2–5°C that were much colder than 6–8°C deep water of Georgia Strait where *L. mandibularis* was usually captured. Similar relationships of cooler temperatures in deep water were also found in Lynn Canal, northern British Columbia inlets, Portland Canal, Astoria Canyon and Monterey Canyon (see Fig. 3 for temperature regimes). In the case of Astoria and Monterey, surface waters may have been considerably warmer, but at depths where the majority of *L. mandibularis* were captured, the temperatures were still cooler because of a sharp thermocline. These data suggest, therefore, that the warmest temperatures inhabited by *L. mandibularis* tend to be the deep waters of Georgia Strait rather than elsewhere such as off southern California. Exceptions include Puget Sound where conditions are somewhat more variable, and the surface of Monterey Canyon where some of the migrating population temporarily occur. In one respect, *L. mandibularis* from Georgia Strait probably cannot seek the lowest range of their preferred temperatures as can other populations because the Strait's deep waters do not have comparably cool water.

The temperature data described here would have been more useful had similar techniques been used for the calculations of temperature means and variation in each area. Although Waldichuck (1957) summarized numerous observations at a number of depth intervals in Georgia Strait (Fig. 3), continuous recordings of temperature (Tabata and Strickland 1972a, b, c) were taken only from four depths (3, 50, 140, and 200 m) at three locations. Data ulilized here for other areas in Fig. 3 were dependant on monthly observations from September 1969 to February 1971 in Lynn Canal (Wing 1976), two sampling periods in Portland Canal (Pickard 1961), 10 observations from nine stations taken between October 16 1952 and February 28 1956 off Seattle in Puget Sound (University of Washington 1954), 8 observations taken between March 27 and October 18 1962 off Astoria Canyon (Love 1963), and numerous observations reported as extreme and mean annual temperatures for Monterey Canyon during 1932–33 (Skogsberg 1936). Although Pickard (1961) reports on only two inlets (Gardner and Kynock) near collection localities of two of the northern British Columbia samples (Fig. 1), he also reports temperatures between 6 and 7°C at 200 m depths for 14 other inlets in northern British Columbia (between Vancouver Island and Portland Canal), and 7–8°C for inlets interconnected with water of the inside passage off northern Vancouver Island compared with 7.5–8.5°C waters at 200 m depths for inlets connected to Georgia Strait. In addition, studies by Dodimead et al. (1963) substantiate the overall generalization of cooler deep waters in the near shore oceanic waters compared with the inland waters of Strait of Georgia. Some year-to-year variation might be expected similar to that off Monterey where variation of deep-water temperatures of as much as 2°C (Broenkow et al. 1975, 1976) occur due to variable strengths of oceanic upwelling, and this may explain, in part, the variation found in the three Monterey samples graphed in Fig. 1.

Salinity Variation

Salinity values were graphed (Fig. 3) in the same manner and from the same references as those previously described for temperature. When compared to Georgia Strait, salinity values for Oregon and California are more divergent than temperature at all depths but the overall pattern is inversely similar to temperature at all localities. Georgia Strait waters are least saline (less than 31‰). Puget Sound has a similar mode but is more variable. The northern waters tend to have somewhat diluted upper layers but are generally more saline (over 31‰) at depths where *L. mandibularis* live. Astoria and Monterey have the most saline waters at all depths and are generally above 32 or 33‰ at depths inhabited by *L. mandibularis*. Therefore, the least saline waters inhabited by *L. mandibularis* are probably those of the Strait of Georgia and the most saline are those off Astoria and Monterey.

Tidal Mixing in Inlets

Previous authors have described major features of water flow in British Columbia's inlets (Herlinveaux and Tully 1961; Pickard 1961; Thomson 1976). Typically, river runoff mixes and entrains seawater as it

flows seaward through the surface layers. Saline waters flow inward along the bottom before passing upward and replacing the surface entrained sea water that has passed seaward. The strength of seaward flowing surface waters depends on the volume of river runoff. Deeper inlets with deep sills at their entrance might have relatively unmixed deep oceanic waters flowing inward but a shallow sill modifies the quality of bottom water in inlets.

In Georgia Strait, sills as shallow as 100 m separate the Strait's inside waters that reach depths up to 700 m. Strong tidal currents at the entrance to Georgia Strait mix the diluted surface waters with saline bottom waters and it is this mixing process that presumably supplies the warmer and relatively dilute deep waters of the Strait. Herlinveaux and Tully (1961) indicate water below 50–75 m in the Strait of Juan de Fuca tends to flow inward, and consequently, one might expect that weakly swimming fishes with young remaining at deeper depths could be entrapped with the incoming deeper water. Diel vertical migration could bring some individuals into the shallower layers of outflowing water, but a greater proportion of their time at depth would tend to perpetuate the filter bridge effect of being entrapped by the incoming water. Because relatively few individuals from Georgia Strait have the same counts as fish from nearby Goletas Channel or Puget Sound, it would appear that there is little movement of *L. mandibularis* between these areas.

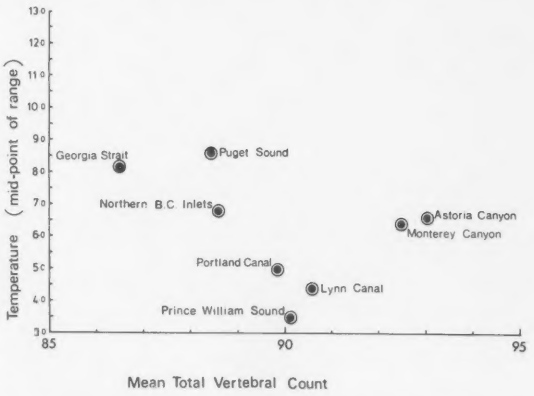

FIG. 4. Approximate mean temperature (taken at same depth at which mode of samples from each locality were captured — see Fig. 3) plotted against mean count of total numbers of vertebrae (see Fig. 1).

Discussion

Barraclough and Waldichuck (1954) first described the probable mechanism by which weakly swimming bathypelagic fishes are passively transported by deeper waters flowing into inlets such as the Strait of Georgia. They also concluded that the deep-water environment of the Strait was not significantly different from the intermediate waters of 100–200 m depths in the nearby Pacific Ocean. *Lycodapus mandibularis* probably occurs more frequently in waters at or below 200 m where the environment is demonstrably different (Fig. 3); however, such migration as occurs off Monterey (Anderson 1977) must yet be demonstrated within the Strait of Georgia. Peden and Anderson (1978) found a preponderance of *L. mandibularis* collections from inlets and submarine canyons with relatively few from intermediate areas. Inflowing deep waters in northern inlets or similar flow from upwelling in southern submarine canyons could provide a simple explanation for *Lycodapus* aggregation if they select deep water and do not move extensively into the surface waters that flow away from the canyons and inlets. Such aggregations could produce genetically identifiable populations if there is little dispersal from inlet to inlet as seems to be the case in Georgia Strait. Whether temperature differences of 2–5°C or salinity differences of 2–4‰ at water depths of embryo and larval development could alone produce populational mean differences of as many as six vertebrae (Fig. 1 and 3) cannot be determined without experimentation.

On the other hand, Lindsey (1961) suggests that observed variation is not always supported by phenotypic experimentation and vertebral numbers are usually the result of an interplay between several genetic and physical factors.

Imprecise data for actual water depth of egg and larval development probably contributes to the weak correlation between vertebrae and temperature or salinity shown in Fig. 4 and 5. As suggested previously, fishing effort has probably been biased toward shallower depths so that *L. mandibularis* from other than Georgia Strait probably predominate in deeper waters at temperatures or salinities more divergent than shown in Fig. 4 and 5. Furthermore, oceanographic data at time of collection of known samples from California (i.e.

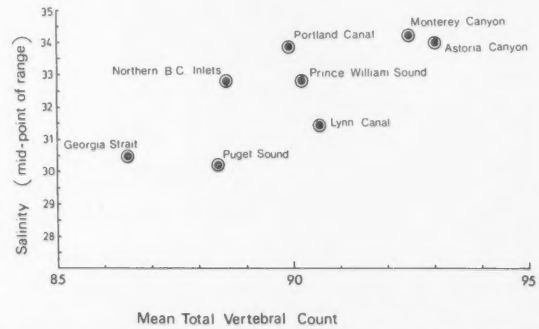

FIG. 5. Approximate mean salinity (taken at same depth at which mode of samples from each locality were captured — see Fig. 3) plotted against mean count of total numbers of vertebrae (see Fig. 1).

La Jolla and Hueneme Canyon, see Peden and Anderson 1978) is desirable since warmer southern water at depth could be expected to disprove the correlation described here. Johnson and Barnett (1975) suggested some midwater fishes in food-poor environments had higher vertebral counts than individuals from more productive areas, because larvae unable to find sufficient food might delay metamorphosis. Slowed growth was presumed to cause an increase in the sensitive period during which vertebral elements were formed. However, measurements of primary productivity are quite similar between the Strait of Juan de Fuca (Lewis 1978) and Monterey Bay (Garrison 1976) or off the Columbia River near Astoria Canyon (Anderson 1972) and Georgia Strait (Parsons et al. 1970) and therefore, Johnson and Barrett's (1975) hypothesis does not seem to apply to *L. mandibularis* in Georgia Strait. Instead, evidence from the present study emphasizes an association of fewer vertebrae associated with higher temperature and/or lower salinity. Inspection of Fig. 4 and 5 even suggests a stronger correlation of vertebral number with salinity than with temperature. On the other hand, such correlates may be merely indicative of other unknown factors that affect vertebral number, and additional experimentation is needed for confirmation. Similarly, whether the presumed correlation is a phenotypic or genetic response to the environment requires additional data.

Most significantly, there are few marine fishes demonstrating the degree of variation described here between populations in British Columbia's various inlets. Consequently, considerable effort was made to delineate the pattern of variation around Vancouver Island but only the Goletas Channel and Johnstone Strait population plus a single specimen off La Perouse Bank were found. One might hypothesize a population in Juan de Fuca Canyon with high counts similar to the nearby Astoria Canyon population and the single La Perouse specimen. The Puget Sound population possibly having continuity to such a Juan de Fuca Canyon population could explain its intermediate counts if stocks also intermixed with nearby Georgia Strait emigrants. Future studies should consider other weakly swimming fishes with similar life histories of young and embryos developing at depth. Preliminary examination of the liparid fishes *Nectoliparis* and *Liparicus* suggests possible correlated features but larger samples are needed. The meristic variation described here does suggest that the deep coastal inlets of western Canada are not homogeneous and do have differing environments affecting the animals that live within them.

Acknowledgments

Several persons have considerably aided this study and special thanks are due to M. E. Anderson of Virginia Institute of Marine Science; W. E. Barraclough and R. Beamish of the Fisheries and Marine Service, Nanaimo, B.C.; R. W. Stewart and Captain A. G. Chamberlain of Institute of Ocean Sciences, Environment Canada, Patricia Bay, B.C.; D. E. McAllister of the National Museum of Canada; D. Stein of Oregon State University; J. C. Quast and E. L. Hall of U.S. Bureau of Commercial Fisheries, Auke Bay, Alaska; and G. Mueller of Institute of Marine Science, University of Alaska who either located critical samples of *L. mandibularis*, added valuable discussion, and/or provided use of X-ray facilities for this study.

ALVERSON, D. C., A. T. PRUTER, AND L. L. RONHOLT. 1964. A study of demersal fishes and fisheries of the northeastern Pacific Ocean. H. R. MacMillan Lectures in Fisheries. Institute of Fisheries, Univ. British Columbia, Vancouver, B.C. 190 p.

ANDERSON, G. E. 1972. Aspects of marine phytoplankton studies near the Columbia River, with special reference to a subsurface chlorophyll maximum, p. 219–240. A. T. Pruter and D. L. Alverson [ed.] *In* The Columbia River estuary and adjacent ocean waters. University of Washington Press, Seattle, Wash.

ANDERSON, M. E. 1977. Systematics and natural history of *Lycodapus mandibularis* in California waters. M.Sc. thesis, California State University at Hayward, Hayward, Calif. 89 p.

BARRACLOUGH, W. E. 1967. Number, size and food of larval and juvenile fish caught with an Isaacs–Kidd trawl in the surface waters of the Strait of Georgia April 25–29, 1966. Fish. Res. Board Can. MS Rep. 926: 1–79.

BARRACLOUGH, W. E., AND J. D. FULTON. 1967. Number, size composition and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4–8, 1966. Fish. Res. Board Can. MS Rep. 940: 1–82.

1968. Food of larval and juvenile fish caught with a surface trawl in Saanich Inlet during June and July 1966. Fish. Res. Board Can. MS Rep. 1003: 1–78.

BARRACLOUGH, W. E., D. G. ROBINSON, AND J. D. FULTON. 1968. Number, size composition, weight, and food of larval and juvenile fish caught with a two-boat surface trawl in Saanich Inlet April 23–July 21, 1968. Fish. Res. Board Can. MS Rep. 1004: 1–305.

BARRACLOUGH, W. E., AND M. WALDICHUK. 1954. Offshore characteristics in the deep waters of the Strait of Georgia as indicated by bathypelagic fish. J. Fish. Res. Board Can. 11: 501–506.

BEAMISH, R. J., M. SMITH, R. SCARSBROOK, AND C. WOOD. 1976. Hake and Pollock Study, Strait of Georgia Cruise *G. B. Reed*, June 16–27, 1975. Fish. Mar. Serv. Data Record, Pacific Biological Station, Nanaimo, B.C. 1: 1–174.

BROENKOW, W. W., S. R. LASLEY, AND G. C. SCHRADER. 1975. California cooperative fisheries investigations hydrographic data report Monterey Bay, July to December, 1974. Moss Landing Marine Laboratories Tech. Publ. 75–1. National Sea Grant Program. 80 p.

1976. California cooperative fisheries investigations hydrographic data report; Monterey Bay, January to December, 1975. Moss Landing Marine Laboratories Tech. Publ. 76–1. National Sea Grant Program. 157 p.

DODIMEAD, A. J., F. FAVORITE, AND J. HIRANO. 1963. Salmon of the North Pacific Ocean, Part II. Review of Oceanography of the Subarctic Pacific Region. Int. North Pac. Fish. Comm. Bull. 13: 1–195.

GARRISON, D. L. 1976. Contribution of the net plankton and nannoplankton to the standing stocks and primary

productivity in Monterey Bay, California during the upwelling season. Fish. Bull. U.S. Dep. Comm. Nat. Mar. Fish. Serv. 74: 183–194.

HERLINVEAUX, R. H., AND J. P. TULLY. 1961. Some oceanographic features of Juan de Fuca Strait. J. Fish. Res. Board Can. 18: 1027–1071.

HUBBS, C. L. 1922. Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of water during development. Am. Nat. 56: 360–372.

HUBBS, C. L., AND C. HUBBS. 1953. An improved graphical analysis and comparison of series of samples. Syst. Zool. 2: 49–56.

JOHNSON, R. K., AND M. A. BARNETT. 1975. An inverse correlation between meristic characters and food supply in midwater fishes: evidence and possible explanations. Fish. Bull. U.S. Dep. Comm. Nat. Mar. Fish. Serv. 73: 284.

JORDAN, D. S. 1891. Relations of temperature to vertebrae among fishes. Proc. U.S. Nat. Mus. 14: 107–120.

LEWIS, A. G. 1978. Concentrations of nutrients and chlorophyll on a cross-channel transect in Juan de Fuca Strait, British Columbia. J. Fish. Res. Board Can. 35: 305–314.

LINDSEY, C. C. 1961. The bearing of experimental meristic studies on racial analyses of fish populations. Proc. Ninth Pac. Sci. Congress, Bangkok. 1957: 54–58.

LOVE, C. M. 1963. The physical chemistry and biology for the northeast Pacific Ocean, Columbia River effluent area. Univ. Wash. Dep. Oceanogr. Tech. Rep. 119 (in five volumes).

MEAD, G. W., E. BERTELSON, AND D. M. COHEN. 1964. Reproduction among deep-sea fishes. Deep-Sea Res. 11: 569–596.

MUENCH, R. D., AND C. M. SCHMIDT. 1975. Variations in the hydrographic structure of Prince William Sound. Univ. Alaska Inst. Mar. Sci. Rep. R75-1: 1–135.

PARSONS, T. R., R. J. LEBRASSEUR, AND W. E. BARRACLOUGH. 1970. Levels of production in the pelagic environment of the Strait of Georgia, British Columbia: A review. J. Fish. Res. Board Can. 27: 1251–1264.

PEDEN, A. E. 1966. Reexamination of two species in the stichaeid genus, *Anoplarchus*. Copeia 1966: 340–345.

PEDEN, A. E., AND M. E. ANDERSON. 1978. A systematic review of the fish genus *Lycodapus* (Zoarcidae) with descriptions of two new species. Can. J. Zool. 56: 1925–1961.

PICKARD, G. L. 1961. Oceanographic features of inlets in the British Columbia mainland coast. J. Fish. Res. Board Can. 18: 907–999.

ROBINSON, D. G., W. E. BARRACLOUGH, AND J. D. FULTON. 1968a. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia June 5–9, 1967. Fish. Res. Board Can. MS Rep. 972: 1–109.

1968b. Number, size composition, weight and food of larval and juvenile fish, caught with a two-boat surface trawl in the Strait of Georgia May 1–4, 1967. Fish. Res. Board Can. MS Rep. 964: 1–105.

ROSENBLATT, R. H. 1963. Some aspects of speciation in marine shore fishes. Syst. Assoc. Publ. 5: 171–180.

SKOGSBERG, T. 1936. Hydrography of Monterey Bay, California, thermal conditions, 1929–1933. Trans. Am. Phil. Soc. New Ser. 29: 1–152.

TABATA, S., AND J. A. STRICKLAND. 1972a. Summary of oceanographic records obtained from moored instruments in the Strait of Georgia 1969–1970. Current velocity and seawater temperature from station H-06. Environ. Can. Water Manage. Serv. Pac. Mar. Sci. Rep. 72-7: 1–131.

1972b. Summary of oceanographic records obtained from moored instruments in the Strait of Georgia 1969–1970. Current velocity and seawater temperature from station H-16. Environ. Can. Water Manage. Serv. Pac. Mar. Sci. Rep. 72-8: 1–144.

1972c. Summary of oceanographic records obtained from moored instruments in the Strait of Georgia 1969–1970. Current velocity and seawater temperature from station H-26. Environ. Can. Water Manage. Serv. Pac. Mar. Sci. Rep. 72-9: 141.

TANING, A. V. 1952. Experimental study of meristic characters in fishes. Biol. Rev. 27: 169–193.

THOMSON, R. E. 1976. Tidal currents and estuarine-type circulation in Johnstone Strait, British Columbia. J. Fish. Res. Board Can. 33: 2242–2264.

UNIVERSITY OF WASHINGTON, DEPARTMENT OF OCEANOGRAPHY. 1954. Physical and chemical data for Puget Sound and approaches. Univ. Wash. Dep. Oceanogr. Tech. Rep. 51: 1–141.

WALDICHUK, M. 1957. Physical oceanography of the Strait of Georgia. J. Fish. Res. Board Can. 14: 321–486.

WING, B. L. 1976. Ecology of *Parathemisto libellula* and *P. pacifica* (Amphipoda: Hyperiidea) in Alaskan coastal waters. Nat. Mar. Fish. Serv. NOAA: Northwest Fish Center, Auke Bay Fish Laboratory, Processed Rep. Auke Bay, Alaska. 266 p.

Influences of Dieldrin on the Growth and Body Composition of Fingerling Rainbow Trout (*Salmo gairdneri*) Fed Oregon Moist Pellets or Tubificid Worms (*Tubifex* sp.)[1]

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PHILLIPS, G. R., AND D. R. BUHLER. 1979. Influences of dieldrin on the growth and body composition of fingerling rainbow trout (*Salmo gairdneri*) fed Oregon Moist Pellets or tubificid worms (*Tubifex* sp.) J. Fish. Res. Board Can. 36: 77–80.

Fingerling rainbow trout (*Salmo gairdneri*) fed tubificid worms (*Tubifex* sp.) grew faster than those fed Oregon Moist Pellets (OMP) over a similar range of rations. Faster growth resulted because trout incorporated protein and fat from tubificids more efficiently than from OMP. Exposure to a sublethal concentration of dieldrin in water (0.18 μg/L) did not affect the protein elaboration of trout fed either diet or fat metabolism in trout fed OMP. However, dieldrin reduced fat elaboration in trout fed tubificids. The dieldrin concentrations in trout exposed to dieldrin in water increased as feeding level (and therefore body fat) increased. The different responses to dieldrin by fish fed these two diets provides evidence that the diet offered to fish can significantly influence the outcome of chronic toxicity tests.

Key words: Rainbow trout, tubificid worms, Oregon Moist Pellets, dieldrin, growth, fat metabolism

PHILLIPS, G. R., AND D. R. BUHLER. 1979. Influences of dieldrin on the growth and body composition of fingerling rainbow trout (*Salmo gairdneri*) fed Oregon Moist Pellets or tubificid worms (*Tubifex* sp.) J. Fish. Res. Board Can. 36: 77–80.

Les fingerlings de truite arc-en-ciel (*Salmo gairdneri*) nourris aux vers tubificides (*Tubifex* sp.) croissent plus rapidement que ceux nourris aux boulettes mouillées d'Orégon (OMP) pour une même gamme de rations. Cette croissance plus rapide est due au fait que les truites incorporent les protéines et les lipides des tubificides plus efficacement que celles des OMP. L'exposition à une concentration sublétale de dieldrine dans l'eau (0,18 μg/L) n'affecte pas la formation de protéines chez les truites nourries à l'un ou l'autre régime, ou le métabolisme des lipides chez les truites nourries aux OMP. Cependant, la dieldrine réduit la formation de lipides chez les truites nourries aux tubificides. Les concentrations de dieldrine dans les truites exposées à cette substance dans l'eau augmentent à mesure que le niveau d'alimentation (et, partant, de lipides corporels) augmente. Ces réactions différentes à la dieldrine de poissons nourris à ces deux régimes sont une preuve que le régime alimentaire offert aux poissons peut influencer de façon significative les résultats d'essais de toxicité chronique.

Received August 16, 1978
Accepted October 27, 1978

Reçu le 16 août 1978
Accepté le 27 octobre 1978

ALTHOUGH the effects of diet on responses of mammals to stress have been well documented (Lee et al. 1964; Tinsley 1966; Boyd 1969; Stoewsand et al. 1970; Shackman 1974), few studies have been conducted that investigate how diet composition influences the response of fish to stress. Mehrle et al. (1974) showed that the acute toxicity of chlordane to rainbow trout was influenced by the type of diet fed before exposure. During chronic exposure, Mehrle et al. (1977) found that toxaphene influenced the growth of channel catfish (*Ictalurus punctatus*) differently depending on the Vitamin C content of the diet.

Our studies using rainbow trout (*Salmo gairdneri*) fed tubificid worms (*Tubifex* sp.) obtained locally from hatchery rearing ponds or a production diet (OMP)[3]

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Printed in Canada (J5349)
Imprimé au Canada (J5349)

were undertaken to observe how these diets, either alone or in combination with a dieldrin stress, might influence growth, protein elaboration, and fat accumulation. Three feeding rates were used because growth response may vary with the plane of nutrition.

Materials and methods — Fertilized rainbow trout eggs were obtained from the Oregon Game Commission's Roaring River Fish Hatchery located near Scio, Oregon. The trout were reared on OMP (Hublou 1963) after hatching, and kept at Oregon State University's Oak Creek Laboratory until reaching a size of approximately 3–4 g. Before the experiment, fish of approximately the same size were individually fed one of the diets for 7 d. The experimental group was chosen from these on the basis of diet acceptance and uniform weight.

Trout were kept in 20-L aquaria divided into four separate 5-L compartments, each compartment housing one trout. Filtered creek water and dieldrin were metered to the experimental aquaria via a series of distribution boxes and manifolds equipped with adjustable siphons. Technical dieldrin (Shell Chemical Corporation 1959) was introduced by passing water through a column of inert sand coated with the pesticide (Chadwick and Kiigemagi 1968). Flow rates through all the aquaria were maintained near 100 mL/min (exchange time 3.3 h). Dissolved oxygen was at least 82% of saturation, temperature averaged 15.1°C, and daily photoperiod was 16 h light:8 h dark. Weekly gas-chromatographic analyses confirmed that the concentration of dieldrin eluted from the column remained relatively constant (80–92 μg/L) throughout the experiment. Biweekly analyses of water from the aquaria showed that the mean dieldrin concentration in the aquaria was 0.18 μg/L (SE = 0.05) and ranged from 0.12 to 0.21 μg/L; dieldrin was not detectable in control water.

At the beginning of the 61-d experiment, four fish were killed, weighed, and placed in a vacuum drying oven for 5 d at 80°C. The initial dry weights of the experimental fish were estimated on the basis of the wet to dry weight ratios of this group. Forty-eight fish were used in the experiment; 24 were held in dieldrin-free water and 24 were exposed continuously to dieldrin. Twelve of the fish in each sub-group were fed tubificid worms and 12 were fed OMP. Feeding rates were calculated as percentages of body weight (dry to dry basis); nominal rates included 2½, 4, and 5½% of body weight per day. Rations were readjusted to fixed percentages of body weight after each weighing period.

Fish were fed each day during the experiment except for the day before weighing. The amounts of OMP and tubificid worms to be fed were weighed to the nearest 0.01 g. Excess moisture on tubificid worms was removed before weighing by blotting with paper towels. Dry weight of subsamples of OMP and tubificid worms were determined each week; the dry weights of food consumed by each fish could then be determined because the fish always consumed the entire ration.

Fish were individually weighed at the onset of the experiment and every 7–10 d thereafter. Before each weighing period, fish were starved for 24 h to allow time for evacuation of previously ingested food. Each fish was blotted dry with a soft, moist cloth, placed in a 1000-mL graduated cylinder containing 50 mL of water and weighed to the nearest 0.01 g; no anesthetic was used.

At the end of the experiment, dried samples of the initial fish, the final experimental fish, the OMP, and the tubificid worms were pulverized in a Wiley Mill and preserved in a desiccator for subsequent proximate analyses.

The proximate composition of each fish was determined in duplicate. The biweekly samples of each diet were individually pooled and analyzed in triplicate. Lipids were extracted by the chloroform–methanol method of Bligh and Dyer (1959); protein was determined using a modification (Ballentine 1957) of the microkjeldahl method; and ash content was determined by burning a 0.1-g sample in a muffle furnace at 600°C for 15 h. Carbohydrate contents of tubificids and OMP were calculated by difference. The energy contents of dry samples were calculated from conversion factors (Baker 1974) for fat (38.5 kJ/g), protein (20.5 kJ/g), and carbohydrate (17.2 kJ/g). Rates of growth, food consumption, protein elaboration, protein consumption, and fat elaboration were computed for each sample and comparisons made between treatments. Fat elaboration rate was compared to food consumption rate rather than fat intake since lipid deposition can be derived from dietary constituents other than lipid. Statistical significance was judged using Student's *t*-test (Steel and Torrie 1960); comparisons were based on treatments having similar consumption rates of a particular dietary constituent.

Results and discussion — Both diets contained nearly the same percentages (on a dry basis) of protein and carbohydrates, but tubificids had a higher percentage of fat whereas OMP contained more ash (Table 1). Others (Embody and Gordon 1924; Phillips et al. 1954; Wood et al. 1957) have found a similar relationship between natural and artificial (production) diets.

In general, as ration increased, fish increased (%) in fat and ash and decreased in protein and water; fish samples did not contain carbohydrate. Fish fed the low rations of both diets gained little or no weight over the 2 mo while the average weight increase (wet weight basis) of fish in the high ration treatments ranged from 78.1 to 98.9%. At the end of the experiment the mean proximate composition for individual treatments were as follows:

	% fat	% protein	% ash
low ration	7.2–9.0	78.2–82.0	12.2–13.3
medium ration	7.7–15.1	73.6–80.5	12.6–15.2
high ration	11.0–14.7	73.2–80.9	14.9–16.5

A comparison of control fish — Control fish fed the highest ration of tubificid worms exhibited significantly higher ($P < 0.10$) energy growth rates (joules of growth

TABLE 1. Proximate composition (dry basis) of the two diets used during the test.

Diet	Percentage composition (dry basis)			
	Fat	Ash	Protein	Carbohydrate[a]
Tubificid	15.0	8.2	59.7	17.1
OMP	10.0	12.2	59.7	18.1

[a]Determined by subtracting total percentage of other three constituents from 100.

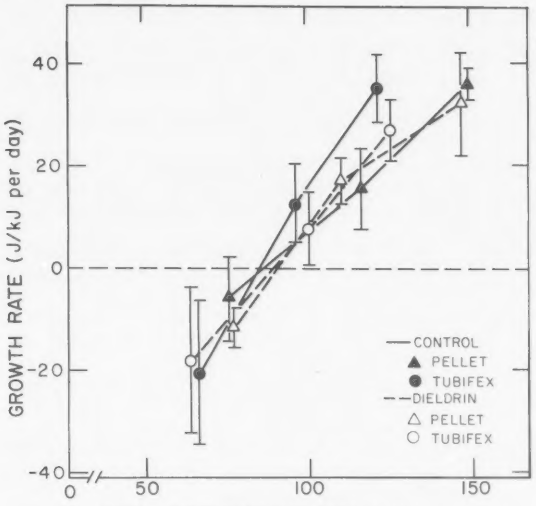

FIG. 1. Influence of dieldrin on the relationship between growth rate and food consumption rate in rainbow trout (*S. gairdneri*) fed Oregon Moist Pellets or tubificid worms; means and 90% confidence intervals shown for each treatment ($n = 4$).

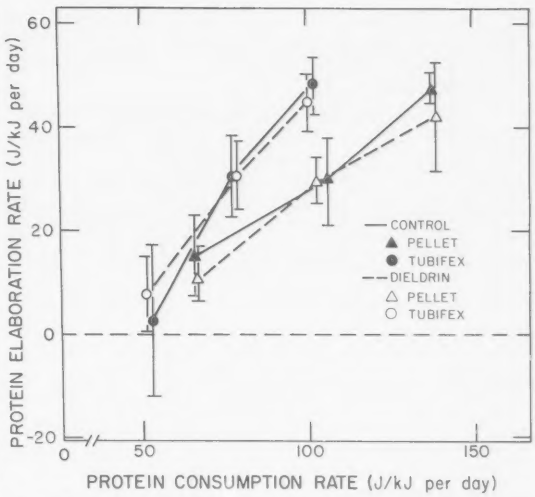

FIG. 2. Influence of dieldrin on the relationship between protein elaboration rate and protein consumption rate in rainbow trout fed Oregon Moist Pellets or tubificid worms; means and 90% confidence intervals shown for each treatment ($n = 4$).

per kilojoule mean trout biomass per day) for a given food consumption rate (joules of food consumed per kilojoule mean trout biomass per day) than fish fed OMP at a comparable rate (Fig. 1). Fish fed the medium ration of OMP averaged a 52.0% weight increase while fish consuming tubificids at a similar rate averaged a 92.6% increase. This occurred because protein and fat from tubificids were more efficiently elaborated than protein and fat from OMP ($P < 0.05$) at the higher feeding rates (Fig. 2 and 3).

Gerking (1955) has pointed out that natural diets are more likely to contain the inorganic nutrients and essential factors necessary for good growth than production diets. The poorer growth of fish fed OMP could result from OMP possessing an inferior quality protein or from a deficiency in some important growth factor such as Vitamin C (Mehrle et al. 1977); a more complete assessment of dietary content is essential to interpret these growth responses.

A comparison of dieldrin-exposed fish — The growth rates of fish fed both diets were not significantly affected by the pesticide, but independent examination of the two major components of growth (fat and protein) revealed that dieldrin significantly depressed the lipid elaboration ($P < 0.05$) of fish fed tubificid worms at the two highest rations fed (Fig. 3). However, dieldrin did not influence fat metabolism of fish fed OMP over the entire range of rations. Moreover, the ability of fish to elaborate protein from either diet was unaffected by

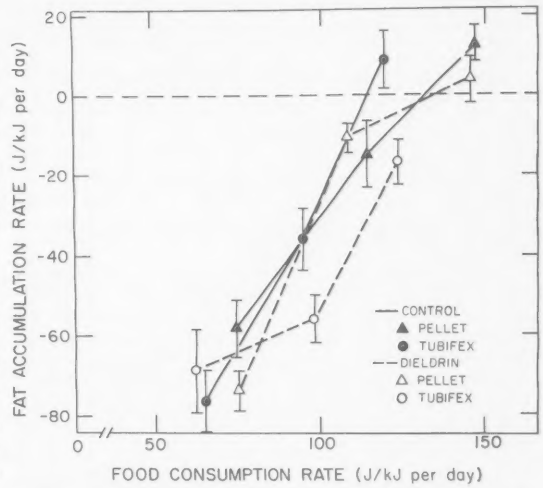

FIG. 3. Influence of dieldrin on the relationship between fat accumulation rate and food consumption rate in rainbow trout fed Oregon Moist Pellets or tubificid worms; means and 90% confidence intervals shown for each treatment ($n = 4$).

the pesticide.

Various species of fish show reduced growth rates when exposed to chlorinated hydrocarbon pesticides. Examples include chinook (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) fed DDT (Buhler et al. 1969), rainbow trout fed endrin (Grant and Mehrle

1973), channel catfish (*Ictalurus punctatus*) fed dieldrin (Argyle et al. 1975), and johnny darters (*Etheostoma nigrum*) immersed in 2.3 μg dieldrin/L (Silbergeld 1973).

Reduced growth in mammals resulting from exposure to dieldrin has been attributed to effects on both carbohydrate and lipid metabolism (Bhatia et al. 1972; Kacew et al. 1973). Increased lipolysis and changes in carbohydrate metabolism induced by dieldrin have also been noted in fish. Silbergeld (1973) observed weight loss and a reduced lipid content in johnny darters exposed to 2.3 μg dieldrin/L for 30 d. The elevated level of fat metabolism associated with increased ingestion of dietary lipids may have increased the vulnerability of the fish fed tubificids to dieldrin, resulting in the observed growth depression.

A limited number of dieldrin analyses on fish exposed to dieldrin in water (one fish per treatment) showed that dieldrin accumulation increased as ration (and therefore fat intake) increased. Dieldrin concentrations (μg/g whole wet fish) were 0.53, 1.55, and 1.65 for the low, medium, and high rations of OMP and 0.47, 0.82, and 1.32 for the low, medium, and high tubificid rations. Reinert (1970) noted a similar relationship between pesticide residues and lipid content in great lakes fishes; this trend presumably results from an increase in the size of the storage reservoir available for lipophilic chlorinated hydrocarbon pesticides.

This study shows that various components of fish growth, such as protein and lipid, are not necessarily influenced in the same way by pesticide exposure; moreover, diet composition and ration can have important influences on the growth responses of fish exposed to a pesticide. Dietary stress interaction should be more critically considered by researchers conducting laboratory studies using fish.

Acknowledgments — We wish to thank Dr I. Tinsley and Dr G. Davis for their helpful editing during the preparation of the manuscript, Dr E. Warren for his suggestions regarding experimental design, and Dr R. R. Claeys for performing the dieldrin analyses. This work was supported by training grant No. 572-WP-208 from the U.S. Environmental Protection Agency and by research grants ES-004 and ES-00210 from the U.S. Public Health Service, National Institute of Health.

ARGYLE, R. L., G. C. WILLIAMS, AND C. B. DANIEL. 1975. Dieldrin in the diet of channel catfish (*Ictalurus punctatus*): Uptake and effect on growth. J. Fish. Res. Board Can. 32: 2197–2204.

BAKER, J. C. 1974. Protein and lipid factors in the bioenergetics of swimming in fish (*Oncorhynchus kisutch*). Ph.D. Thesis. Oregon State University, Corvallis, Oreg. 112 p.

BALLENTINE, R. 1957. Determination of total nitrogen and ammonia, p. 984–995. *In* S. P. Colowick and N. O. Kaplan [ed.] Methods in enzymology. Vol. 3. Academic Press, Inc., New York, N.Y.

BHATIA, S. C., S. C. SHARMA, AND T. A. VENKITASUBRAMANIAN. 1972. Acute dieldrin toxicity: Biomedical changes in the blood. Arch. Environ. Health 24: 369–372.

BLIGH, E. G., AND W. J. DYER. 1959. Extraction of lipids from animal sources. Can. J. Biochem. Physiol. 37: 911–917.

BOYD, E. M. 1969. Diet and drug toxicity. Clin. Toxicol. 2: 423–433.

BUHLER, D. R., M. E. RASMUSSON, AND W. E. SHANKS. 1969. Chronic oral DDT toxicity in juvenile coho and chinook salmon. Toxicol. Appl. Pharmacol. 14: 535–555.

CHADWICK, G. C., AND U. KIIGEMAGI. 1968. Toxicity evaluation of a technique for introducing dieldrin into water. J. Water Pollut. Control Fed. 40: 76–82.

EMBODY, G. C., AND M. GORDON. 1924. A comparative study of natural and artificial foods of brook trout. Trans. Am. Fish. Soc. 54: 185–200.

GERKING, S. D. 1955. Influence of rate of feeding on body composition and protein metabolism of bluegill sunfish. Physiol. Zool. 28: 267–282.

GRANT, B. F., AND P. M. MEHRLE. 1973. Endrin toxicosis in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 31–40.

HUBLOU, W. F. 1963. Oregon pellets. Progr. Fish-Cult. 25: 175–180.

KACEW, S., D. J. B. SUTHERLAND, AND R. L. SINGHAL. 1973. Biochemical changes following chronic administration of heptachlor, heptachlor epoxide, and endrin to male rats. Environ. Physiol. Biochem. 3: 211–229.

LEE, M., K. HARRIS, AND H. TROWBRIDGE. 1964. Effect of the level of dietary protein on the toxicity of dieldrin for the laboratory rat. J. Nutr. 84: 136–144.

MEHRLE, P. M., W. W. JOHNSON, AND F. L. MAYER. 1974. Nutritional effects on chlordane toxicity in rainbow trout. Bull. Environ. Contam. Toxicol. 12: 513–517.

MEHRLE, P. M., F. L. MAYER, AND W. W. JOHNSON. 1977. Diet quality in fish toxicology: Effects on acute and chronic toxicity, p. 269–280. *In* F. L. Mayer and J. L. Hamelink [ed.] Aquatic toxicology and hazard evaluation. Am. Soc. Testing and Materials, ASTM STP 634.

PHILLIPS, A. M., R. S. NIELSON, AND D. R. BROCKWAY. 1954. A comparison of hatchery diets and natural food. Progr. Fish-Cult. 16: 153–157.

REINERT, R. E. 1970. Pesticide concentrations in great lakes fish. Pestic. Monit. J. 3(4): 233–240.

SHACKMAN, R. A. 1974. Nutritional influences on the toxicity of environmental pollutants. Arch. Environ. Health 28: 105–113.

SHELL CHEMICAL CORPORATION. 1959. Handbook of aldrin, dieldrin, and endrin formulations. The Woodrow Press, Inc., New York, N.Y. 195 p.

SILBERGELD, E. K. 1973. Dieldrin. Effects of chronic sublethal exposure on adaptation to thermal stress in freshwater fish. Environ. Sci. Technol. 7: 846–849.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York, N.Y. 481 p.

STOEWSAND, G. S., E. V. BRODERICK, AND V. B. BOURKE. 1970. Dietary protein and dieldrin toxicity. Ind. Med. Surg. 39: 45–49.

TINSLEY, I. J. 1966. Nutritional interaction of dieldrin toxicity. J. Agric. Food Chem. 14: 563–566.

WOOD, E. M., W. T. YASUTAKE, A. N. WOODALL, AND J. E. HALVER. 1957. The nutrition of salmonoid fishes. II. Studies on production diets. J. Nutr. 61: 479–488.

Comparison of a High Volume Pump and Conventional Plankton Nets for Collecting Fish Larvae Entrained in Power Plant Cooling Systems

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LEITHISER, R. L., K. F. EHRLICH, AND A. B. THUM. 1979. Comparison of a high volume pump and conventional plankton nets for collecting fish larvae entrained in power plant cooling systems. J. Fish. Res. Board Can. 36: 81–84.

A high volume pump (2.5 m^3/min capacity at 6 m head) and conventional plankton nets (0.5 and 1.0 m diam) were operated side by side in two tests to evaluate the efficiency of each gear for sampling fish larvae within the intake structure of a coastal power plant. At intake channel current velocities up to 40 cm/s (the maximum tested), the pump in one test caught significantly more fish larvae than the nets. Compared to the pump, both sizes of plankton nets in each test greatly undersampled large larvae (over 5.0 mm total length). Our findings suggest that conclusions regarding ichthyoplankton entrainment based on data obtained with conventional plankton nets may be of questionable validity.

Key words: ichthyoplankton, entrainment, pump, nets

LEITHISER, R. L., K. F. EHRLICH, AND A. B. THUM. 1979. Comparison of a high volume pump and conventional plankton nets for collecting fish larvae entrained in power plant cooling systems. J. Fish. Res. Board Can. 36: 81–84.

Au cours de deux essais en vue d'évaluer l'efficacité de chaque échantillonneur de larves de poissons à l'intérieur de la prise d'eau d'une centrale électrique côtière, nous avons placé côt-à-côte une pompe à gros volume (capacité de 2,5 m^3/min avec charge de 6 m) et des filets à plancton (0,5 m et 1,0 m de diamètre). A des vitesses de courant dans le chenal d'entrée allant jusqu'à 40 cm/s (le maximum testé), la pompe captura dans un essai des quantités de larves de poissons nettement plus grandes que les filets. Comparés à la pompe, les filets à plancton des deux grosseurs capturèrent des quantités beaucoup moins grandes de grosses larves (longueur totale dépassant 5,0 mm). Nos résultats donnent à croire que les conclusions concernant l'entraînement de l'ichtyoplancton fondées sur des données obtenues à l'aide de filets à plancton conventionnels peuvent avoir une validité douteuse.

Received July 31, 1978
Accepted October 17, 1978

Reçu le 31 juillet 1978
Accepté le 17 octobre 1978

ASSESSMENT of ichthyoplankton entrainment by power generating stations that use once-through cooling systems is required in the United States by Section 316(b) of the United States Federal Water Quality Control Act Amendments (P.L. 92-500). The traditional approach to sampling ichthyoplankton of towing single or paired nets through the water at an optimal velocity is usually unsuitable for sampling within power plant intake channels and conduits because of space restrictions. Previous entrainment studies have used stationary plankton nets (Lauer et al. 1974; Marcy 1976) or relatively low volume pumps (Davies and Jensen 1974; Jude 1976) to sample the intake water. Many power plants use intake flow rates through the traveling screens of only 15–30 cm/s (Bibko et al. 1974; Lauer et al. 1974), which are generally below that considered optimal for fishing efficiency (Ahlstrom et al. 1973). Thus, estimates of larval fish entrainment based on stationary plankton net samples may be biased due to sampler avoidance. Most pump systems used in previous entrainment studies may have been of limited value for sampling fish larvae because of their comparatively low pumping rates (usually less than 0.75 m^3/min).

This report describes the sampling efficiency of a pump designed to operate at flow rates greater than 2.0 m^3/min and to cause minimal damage to organisms. Pump-collected samples are compared to ones obtained simultaneously with 1.0-m (335-μm mesh) and 0.5-cm (363-μm mesh) diam plankton nets operated in fixed positions in a power plant's intake at current velocities up to 40 cm/s. Two comparisons were made, one in July and the other in December 1977.

Materials and methods — The high volume pump assembly used in this study consists of a collection tank (2 m^3), a 25-hp Onan gasoline engine, a Gast electric vacuum pump (used for priming main pump), and a Paco fish transfer pump (Fig. 1). Water from the pressure side of the pump is discharged below the surface into the collection tank. The water flows over a weir after flowing through a 335-μm mesh net, and is discharged through a 20-cm ID hose. The height of water flowing over a weir determines pump flow rates; calibration of the weir was

Printed in Canada (J5330)
Imprimé au Canada (J5330)

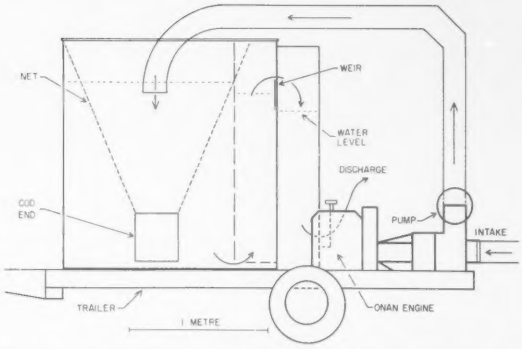

FIG. 1. High volume ichthyoplankton pump mounted on trailer.

achieved by determining the time required to fill a known volume at various flow rates.

Collections made with two conventional plankton nets (a 0.5-m diam, 363-μm mesh conical design and a 1.0-m diam, 335-μm mesh cylinder–cone design) were compared to the pump-collected samples. Flow rates through the nets were measured with calibrated TSK and General Oceanics flow meters located slightly off-center in the 1.0- and 0.5-m diam nets, respectively. The TSK meter was calibrated over a range of low current velocities (13–52 cm/s) at the Lockheed Ocean Laboratory towing basin in San Diego and the General Oceanics meter was calibrated by a series of paired tows with the TSK meter.

Two comparisons of the pump with nets were conducted at a coastal power plant in Southern California. Pump samples were collected at one side of the cooling water intake channel while plankton net samples were collected simultaneously on the opposite side of the channel (approximately 8 m apart) by suspending nets in the intake current. The intake structure at the region sampled is symmetrical and no obvious flow patterns or other conditions were observed which might have caused a nonrandom distribution of plankton across the channel. All test comparisons were conducted at night at the same depth (0.5–1.5 m). During the first study (July 20–21, 1977) ten samples each were collected with the pump and the 1-m diam net. The plankton net was operated for 10 min midway through each 30-min pump sample. The net filtered approximately 1.5–3 times more than the pump depending on the intake channel current velocity. Intake channel flow velocity averaged 26 cm/s during this series and ranged from 19 to 40 cm/s. Ten comparisons were made in the second study (December 7–8, 1977), with both 0.5- and 1.0-m diam nets side by side operating simultaneously with the pump for the entire 30-min sampling period. Intake channel flow velocity during the second study averaged 30 cm/s and ranged from 22 to 40 cm/s. Plankton samples were preserved in the field in buffered 5% formalin in seawater and subsequently sorted in the laboratory for fish larvae. A Folsom plankton splitter was used to obtain $\frac{1}{2}$–$\frac{1}{4}$ aliquots for samples containing more than approximately 500 larvae.

Results and discussion — During the first study the pump collected a total of 1874 larvae (625 m^3 of seawater filtered). Pump samples indicated a higher density of larvae (number per cubic metre filtered) than did plankton net samples in 7 out of 10 trials. The average number of total larvae collected per cubic metre filtered for pump samples was greater than that obtained with the 1-m diam net although Wilcoxon's signed-ranks test showed that the difference was not statistically significant (Table 1). The average density of large larvae (over 5 mm TL) calculated from pump samples, however, was significantly greater than the value obtained for 1-m plankton net samples (Table 1). Furthermore, 10.8% of the pump-caught larvae were longer than 5 mm in contrast to only 1.6% of the net-caught larvae. These data suggest that the pump and plankton net sampled small larvae equally well, but larger larvae, which are better swimmers, may have been more successful at avoiding the plankton net than the pump intake. The condition of pump-caught larvae (all sizes) was similar to that of larvae in net samples.

TABLE 1. Summary of larval densities measured by pump and 1.0- and 0.5-m nets as described in text.

Statistic	Total density (no./m^3)			Density > 5 mm TL (no./m^3)			Sample volume (m^3)			Current velocity (cm/s)
	1.0-m Net	Pump	0.5-m Net	1.0-m Net	Pump	0.5-m Net	1.0-m Net	Pump	0.5-m Net	
				Study 1 (July 20–21, 1977)						
Mean	2.56	3.01	N.D.[a]	0.04	0.32	N.D.[a]	121	62	N.D.[a]	26
SD	2.16	1.46	N.D.[a]	0.05	0.16	N.D.[a]	28	2	N.D.[a]	6
n	10	10	N.D.[a]	10	10	N.D.[a]	10	10	N.D.[a]	10
P		>0.1	N.D.[a]		<0.01	N.D.[a]		—	—	
				Study 2 (Dec. 7–8, 1977)						
Mean	1.44	1.83	0.70	0.19	0.40	0.10	414	64	105	30
SD	0.86	0.75	0.25	0.09	0.17	0.06	83	1	28	6
n	9[b]	10	10	9[b]	10	10	9[b]	10	10	10
P		<0.05	<0.01		<0.01	<0.01		—	—	

[a]N.D. means no data collected. The 0.5-m net was not used in the first study.
[b]One sample was not analyzed due to inadequate preservation.

TABLE 2. Relative abundance (%) of common larval fish families collected during pump–net comparisons.

Families	Pump samples		1.0-m Net samples		0.5-m Net samples[a]	
	Larvae < 5 mm TL	Larvae ≥ 5 mm TL	Larvae < 5 mm TL	Larvae ≥ 5 mm TL	Larvae < 5 mm TL	Larvae ≥ 5 mm TL
			Study 1			
Gobiidae	56.1	1.4	67.9	—		
Blenniidae	22.4	—	17.3	—		
Sciaenidae	1.0	5.9	1.6	—		
Atherinidae	—	1.7	—	0.3		
Clinidae	1.8	0.6	0.1	—		
Syngnathidae	—	1.2	—	1.3		
Other taxa and unidentified larvae	7.9	—	11.5	—		
			Study 2			
Gobiidae	76.3	0.6	82.2	0.1	77.7	0.1
Atherinidae	—	14.4	—	11.8	—	11.4
Clinidae	0.5	6.8	0.1	1.6	0.2	2.9
Engraulidae	0.2	0.2	1.6	0.2	2.8	0.1
Other taxa and unidentified larvae	1.0	—	2.4	—	4.8	—

[a]No samples taken with the 0.5-m net during the first study.

The comparatively low catch of larger larval fishes by the plankton nets is not explained by clogging of the net, since plankton abundance was relatively low throughout the study and nets never appeared to clog. In view of the slow channel current velocity and relatively small filter mesh, it is unlikely that extrusion through the mesh would account for the low catch of large larvae by the plankton nets.

During the second study, a total of 1170 larvae (639 m^3 filtered) was collected with the pump, while 1.0- and 0.5-m net catches were 5234 larvae (3634 m^3 filtered) and 721 larvae (1044 m^3 filtered), respectively. In 8 out of 10 comparisons, pump samples indicated a higher density of larvae than did plankton net samples. Wilcoxon's signed-ranks tests showed that the mean density of total larvae and of those over 5 mm TL obtained with the pump were significantly greater than those obtained using either of the plankton nets (Table 1). As expected, from the findings of McGowan and Fraundorf (1966), the 1-m diam net consistently sampled more efficiently than the 0.5-m net. Mean larval density values obtained with the 1.0-m net were twice as high as those obtained with the 0.5-m net (Table 1). Although mesh size in the 0.5-m diam net (363 μm) was slightly larger than the 1.0-m diam net (335 μm), differential retention of larvae probably did not occur, since all larvae were sufficiently large to be retained by the 363-μm mesh.

It was expected that the ability of larvae to avoid capture would decrease with increasing intake channel velocity, but no significant correlation was found between current velocity and catch per cubic meter filtered for either pump or net samples; in every case $P > 0.05$. The comparisons of total larvae and of those larger than 5 mm TL with current velocity were made by Spearman's rank-correlation, the coefficients of which are listed below.

Study	Pump		1.0 m Net		0.5 m Net	
	Total	≥ 5 mm TL	Total	≥ 5 mm TL	Total	≥ 5 mm TL
1	−0.11	−0.24	−0.12	0.34	—	—
2	0.02	0.55	−0.26	0.48	−0.24	0.33

The lack of significant correlation may have been due to the small range of velocities tested and the large scale variability in larval abundance through time.

The composition of samples collected by both techniques during the first study were similar (Table 2), but sciaenid larvae, which were generally large and well developed, were undersampled by the net. During the second study the relative abundance of major taxa collected was similar among all three samplers, although larger size categories generally were poorly represented in net samples (Table 2). Virtually all of the larvae collected were from demersally spawning fish. In the first study this group accounted for at least 82.5% of the pump sampled larvae and 86.9% of those caught with the 1.0-m net. The percentages were even higher in the second survey, 98.6% from the pump and 95.8% from the 1.0-m net. Off Southern California, the inshore demersal spawners live and reproduce in a narrow coastal band. If excessive numbers of the young of these fishes are entrained by power plants, this might constitute a problem for some populations of inshore fishes.

The data from the two surveys indicates that in power plant intake channels the high volume pump is a more effective larval fish sampler than conventional

plankton nets operated at intake current velocities up to 40 cm/s*. Large actively swimming larvae were sampled less efficiently by both sizes of plankton nets. The 0.5-m net was the least effective for collecting larval fishes at all velocities tested. This is similar to the findings of Aron (1958) who reported a 1.5 m^3/min (400-U.S. gpm) pump to be a more efficient sampler of copepods than a 0.5-m net. Furthermore, it appears that many individuals of species with large, well-developed larvae at hatching may be missed entirely by 0.5- and 1.0-m plankton nets under the confines of sampling within a power plant. Our findings should be considered with respect to the common practice of trying to assess power plant entrainment of fish larvae by suspending 0.5- or 1.0-m diam plankton nets in slow moving intake currents. Thus, conclusions regarding ichthyoplankton entrainment based on data obtained with conventional plankton nets may be of questionable validity. However, the sampling efficiency of plankton nets would be expected to improve at higher current velocities (Tranter et al. 1968), and further testing is required to establish which technique (pump or net) is superior at higher speeds.

Acknowledgments — We thank Dr Paul Smith of the National Marine Fisheries Service in La Jolla, California for critically reviewing the manuscript. Thanks is also given to G. Muszynski for the art work and to D. McDermott-Ehrlich for editorial comments.

AHLSTROM, E. H., K. SHERMAN, AND P. SMITH. 1973. Seagoing operation in ichthyoplankton surveys. *In* G. Hempel [ed.] Fish egg and larval surveys (contributions to a manual). FAO Fish. Tech. Rap. No. 122.

ARON, W. 1958. The use of a large capacity portable pump for plankton sampling, with notes on plankton patchiness. J. Mar. Res. 16: 158–173.

BIBKO, P. N., L. WIRTENAN, AND P. E. KUESER. 1974. Preliminary studies on the effects of air bubbles and intense illumination on the swimming behavior of the striped bass (*Morone saxitalis*) and the gizzard shad (*Dorosoma cepedianum*), p. 293–304. *In* L. D. Jensen [ed.] Second workshop on entrainment and intake screening. Edison Electric Inst. Rep. 15.

DAVIES, R. M., AND L. D. JENSEN. 1974. Entrainment of zooplankton at three mid-Atlantic power plants, p. 131–155. *In* L. D. Jensen [ed.] Second workshop on entrainment and intake screening. Edison Electric Inst. Rep. 15.

JUDE, D. J. 1976. Entrainment of fish larvae and eggs on the Great Lakes, with special reference to the D. C. Cook Nuclear Plant, Southeastern Lake Michigan, p. 177–199. *In* L. D. Jensen [ed.] Third national workshop on entrainment and impingement. Section 316(b) — research and compliance.

LAUER, G. J., W. T. WALLER, D. W. BATH, W. MEEKS, D. HEFFNER, T. GINN, L. ZUBARIK, P. BIBKO, AND P. C. STORM. 1974. Entrainment studies on Hudson River organisms, p. 37–82. *In* L. D. Jensen [ed.] Second workshop on entrainment and intake screening. Edison Electric Inst. Rep. 15.

MARCY, B. C. 1976. Planktonic fish eggs and larvae of the lower Connecticut River and the effects of the Connecticut Yankee Plant including entrainment, p. 115–139. *In* D. Merriman and L. M. Thorpe [ed.] The impact of a nuclear power plant. River ecological study. Am. Fish. Soc. Monogr. No. 1: 252 p.

MCGOWAN, J. A., AND V. J. FRAUNDORF. 1966. The relationship between size of net used and estimates of zooplankton diversity. Limnol. Oceanogr. 11: 456–469.

TRANTER, D. J., J. D. KERR, AND A. C. HERON. 1968. Effects of hauling speed on zooplankton catches. Aust. J. Mar. Freshwater Res. 19: 65–75.

*Even the maximum current velocity observed in this study was well below the speed at which plankton nets are ordinarily towed at sea. It is not the authors' intent to extrapolate these results to sampling at sea.

Sublethal Effects of Environmental Acidification on Rainbow Trout (*Salmo gairdneri*)

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NEVILLE, C. M. 1979. Sublethal effects of environmental acidification on rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 36: 84–87.

Dorsal aorta blood samples were taken from cannulated rainbow trout (*Salmo gairdneri*) exposed to pH 4.0 (acid group) or pH 7.0 (controls) in normocapnic conditions at 10°C. Over a 5-d period there was a significant gradual decrease in pH and total CO_2 in the acid group but no significant difference in pO_2 and lactate compared to the controls. After uncannulated rainbow trout were exposed to the same conditions for 12 d there were significant increases in hemoglobin, hematocrit, and erythrocyte levels in caudal vein samples from the acid group. The results show that rainbow trout exposed to acid

Printed in Canada (J5317)
Imprimé au Canada (J5317)

without hypercapnia develop acidaemia which is not a result of anaerobic respiration. The increase in erythrocyte concentration probably offsets the effects of acidaemia upon blood oxygen carrying capacity. Differences in ambient pCO_2 and/or species differences could account for varying acid-base values in acid exposed fish reported by different workers.

Key words: environmental acidification, acidaemia, lactate, pH, total carbonate, fish

NEVILLE, C. M. 1979. Sublethal effects of environmental acidification on rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 36: 84–87.

Nous avons prélevé des échantillons de sang de l'aorte dorsale de truites arc-en-ciel (*Salmo gairdneri*) munies d'une canule et exposées à un pH de 4,0 (groupe acide) ou un pH de 7,0 (témoins) dans des conditions normocapniques à 10°C. Sur une période de 5 d, on observe un déclin graduel significatif du pH et du CO_2 total dans le groupe acide, mais pas de différence dans le pO_2 et le lactate, comparativement aux témoins. Après exposition de truites arc-en-ciel dépourvues de canules aux mêmes conditions durant 12 d, il y a élévation significative des niveaux d'hémoglobine, d'hématocrite et d'érythrocytes dans les échantillons prélevés dans la veine caudale du groupe acide. Ces résultats démontrent que les truites arc-en-ciel exposées à l'acide sans hypercapnie subissent une acidémie qui n'est pas le résultat de la respiration anaérobie. Il est probable que l'augmentation de la concentration d'érythrocytes contrebalance les effets de l'acidémie sur la capacité de transport d'oxygène du sang. Des différences dans le pCO_2 ambiant et/ou des différences spécifiques pourraient expliquer les valeurs variables d'acide-base signalées par différents chercheurs chez des poissons exposés à l'acide.

Received July 25, 1978
Accepted October 13, 1978

Reçu le 25 juillet 1978
Accepté le 13 octobre 1978

UNTIL the 1960s unnatural acidification of freshwater systems was due mainly to industrial effluents or acid drainage from mines and thus was confined to predictable areas. However, in the past decade there have been many reports of precipitation contaminated by atmospheric pollution causing acidification of soft water lakes in widespread hitherto unpolluted areas (Beamish and Harvey 1972; Likens et al. 1972; Dovland et al. 1976; Oden 1976; Dillon et al. 1978). The resultant depletion of fish populations has led to many studies on the pH tolerance of fish during early stages of development. As the acidity of lakes increases, studies on the physiological effects of acidification on adult fish are becoming increasingly important. Concentrations of acid which are lethal to adult fish have been shown to cause acidaemia and/or electrolyte loss (Lloyd and Jordan 1964; Packer and Dunson 1970; Lievestad and Muniz 1976), whilst the major consequences of long-term sublethal concentrations appear to be electrolyte loss (Lievestad et al. 1976) or Ca^{++} loss in females (Beamish et al. 1975; Lockhart and Lutz 1976). Very few studies have been done to show the progressive sublethal effects of acidification which allow for more detailed physiological investigation. The purpose of this study was to determine the progressive acid-base response of rainbow trout exposed to acidification in an aerated soft water system.

Materials and methods — Rainbow trout (*Salmo gairdneri*, 310–400 g) were obtained from the Franklin Trout Farm, Mount Albert, Ontario and held unfed in running, dechlorinated Toronto tap water at 10 ± 1°C at least 6 d before experimentation.

During the experiments the fish were kept at rest in individual chambers which confined but did not restrain them. Aerated, dechlorinated Toronto tap water was recirculated through the chambers at 800 mL/min at 10 ± 1°C. The pH was maintained within 0.1 units of the required pH using an automatic pH stat system. Ambient pCO_2 was monitored before, during, and after acidification at 10°C with a pCO_2 electrode (Radiometer E 5036) and acid–base analyzer. With the calibrating gases available the lowest detectable pCO_2 was 1.5 mm Hg. Activated charcoal caused a slight increase in water pCO_2 when used for filtration immediately after acidification, so glass wool only was used for 2 d before activated charcoal was included.

The fish were anesthetised with MS 222 and the dorsal aorta was cannulated (Smith and Bell 1964). After a 20 h recovery period at pH 7.0 a 0.3-mL control blood sample was taken before the ambient pH of the experimental group was changed abruptly to 4.0 using 1 mol/L HCl. Controls were kept at pH 7.0 throughout. Because Toronto tap water has a $CaCO_3$ content of about 85 mg/L, acidification led to an acute rise in water pCO_2 from <1.5 to ≈ 15 mm Hg causing a hypercapnic response in the fish lasting 1–2 h. During that time, as the water was well aerated, the CO_2 was driven off and the pCO_2 dropped to <1.5 mm Hg. (The fish made no response during acidification in later experiments when freshly decarbonated Toronto tap water was used.) As the water was recirculated there was no further rise in pCO_2 so the total carbonate content became equivalent to that of a soft water system. The fish remained calm during the rest of the experiment and no coughing or increase in ventilation was seen. Decarbonated water was used at the onset of the experiment for the control fish. Decarbonation involved acidifying to pH 4.0 with 1 mol/L HCl, aerating until the pCO_2 dropped to below 1.5 mm Hg, then titrating back to the original pH with 1 mol/L NaOH.

A 0.3-mL blood sample was drawn on each of the 5 days following acidification. Some samples were not obtained due to cannula failure. Arterial blood pH and pO_2 were measured anaerobically at 10°C using a Radiometer microelectrode unit (E 5021) and pO_2 electrode, respectively. Outputs were recorded on a Radiometer acid–base analyser.

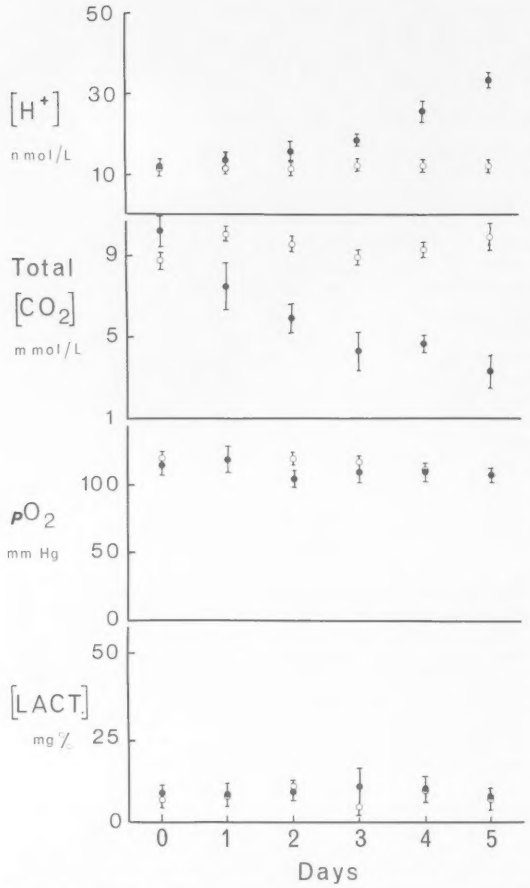

FIG. 1. Arterial blood acid–base values (mean ± SE) in cannulated rainbow trout during 5-d exposure to pH 4.0 (acid group, ●) or pH 7.0 (controls, ○); n ⩾ 6 except day 3 (n = 4), day 4 (n = 2), day 5 total CO_2 and pO_2 (n = 4). For days 1–5, H^+ and total CO_2 of the acid group were significantly different from the controls at 0.001 level, except day 1 H^+ (significantly different at 0.05 level). All other values were not significantly different. Wilcoxon nonparametric ranked sum test.

Total blood CO_2 content was measured by the method of Cameron (1971) and blood lactate was measured by the method of Barker and Summerson (1941) on 0.1 mL blood deproteinized with 0.9 mL 7% perchloric acid.

Hemoglobin, hematocrit, and erythrocyte counts were estimated on caudal vein samples from uncannulated rainbow trout exposed to the same experimental conditions for 12 d. Hemoglobin was measured with an American Optical Hemoglobinometer, hematocrit in microhematocrit tubes centrifuged at 13 000 *g* for 5 min and erythrocytes were counted using an Improved Neubauer counting chamber.

Wilcoxon's nonparametric ranked sum test was used for statistical analysis of the results because of the small number of values obtained on days 3 and 4.

Results — Figure 1 shows that there was a gradual increase in H^+ ion concentration and decrease in total CO_2 concentration of the acid group compared to the control fish. By day 2 the difference between control and acid groups in both parameters was significant at the 0.001 level. There were no significant differences in pO_2 or lactate levels throughout the experiment. In the uncannulated fish after 12-d exposure to acid the hemoglobin, hematocrit, and erythrocyte counts had increased and were significantly different from the controls ($P < 0.05$). Respective values (mean and standard error) were 7.4 ± 0.3 g%, 64 ± 5.0%, and 1.9 ± 0.4 × 10^6/mm^3 for the acid group and 5.6 ± 0.4 g%, 37 ± 3.1%, and 1.2 ± 0.6 × 10^6/mm^3 for the controls.

Discussion — It is apparent that adult rainbow trout exposed for several days to pH 4.0 in a well aerated, recirculating system do become acidaemic but the cause of the acidaemia has not yet been established. It cannot be due to lactic acid accumulation resulting from anaerobic respiration (Fig. 1). In another study Neville (unpublished data) suggested that it could be due to loss of HCO_3^- from the fish into the almost HCO_3^--free acid environment, coupled with a reduced ability to excrete H^+ ions. This is reflected in the depression of total CO_2 levels in the present study. The same experiments showed no difference in tissue water content between control and acidified fish after 12 d exposure. Thus, the increase in hemoglobin, hematocrit, and erythrocyte concentrations found in this study are unlikely to be a result of water redistribution between plasma and tissue compartments. The increase in erythrocyte concentration by approximately 50% within a period of only 12 d is in agreement with a study by Vaala and Mitchell (1970) in which a reduction in venous oxygen tension was met by an increased erythrocyte concentration in brook trout (*Salvelinus fontinalis*) exposed to pH 3 to 4 for 4 d. It suggests that to supplement erythropoiesis extra red cells were released from storage tissues to offset the reduced affinity and capacity of the hemoglobin brought about by the acidaemia, (Bohr and Root effects), and/or to increase the buffering capacity of the blood. The increase in hemoglobin level, maintenance of arterial pO_2, and constancy of blood lactate levels suggest that there was no hypoxic stress despite the acidaemia.

In other papers reporting laboratory studies on the effects of sublethal environmental acidification on adult fish Janssen and Randall (1975) report a decrease in arterial pH in rainbow trout (*Salmo gairdneri*) exposed to pH 5.0 in soft water, but give no data. Acidaemia and loss of total carbonate have not been found in brook trout (*Salvelinus fontinalis*) exposed to an ambient pH of 4.2 for 5 d (Dively et al. 1977) nor apparently in brown trout (*Salmo trutta*) at pH 4.0 for 8 d (Lievestad et al. 1976) although, again, the latter workers do not report their acid–base data. However,

they have shown that both species are more acid tolerant than rainbow trout.

It is also possible that Dively et al. (1977) subjected their fish to increased ambient pCO_2 as well as H^+ ion concentration since their arterial pCO_2 values were elevated. In rainbow trout I have shown that mild hypercapnia ($pCO_2 \approx 4.5$ mm Hg) accompanying environmental acidification prevents acidaemia and loss of total CO_2 (C. M. Neville unpublished data). In reporting results of laboratory studies on exposure to acidity it is therefore essential to specify the pCO_2 as well as the pH of the ambient water.

In the field, the actual water pH at which acidaemia occurs will therefore probably vary with both the species of fish and the ambient pCO_2. The latter will depend on water alkalinity, the amount of aquatic vegetation, benthic population, the depth of water, and the time of year. Other contaminants such as heavy metals may also influence the pH at which acidaemia occurs. Thus, it is hardly surprising that different workers have presented widely varying physiological data for natural fish populations inhabiting acid lakes and for laboratory studies (Lloyd and Jordan 1964; Packer and Dunson 1970; Janssen and Randall 1975; Lockhart and Lutz 1976; Lievestad et al. 1976; Dively et al. 1977).

Acknowledgments — This investigation was supported by a National Research Council of Canada operating grant to Dr G. F. Holeton and a NRC Postgraduate Scholarship to the author. I thank Dr C. M. Wood for helpful criticisms of the manuscript.

BARKER, S. B., AND W. H. SUMMERSON. 1941. The colorimetric determination of lactic acid in biological material. J. Biol. Chem. 138: 535–554.

BEAMISH, R. J., AND H. H. HARVEY. 1972. Acidification of the La Cloche Mountain Lakes, Ontario and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

BEAMISH, R. J., W. L. LOCKHART, J. C. VANLOON, AND H. H. HARVEY. 1975. Long-term acidification of a lake and resulting effects on fishes. Ambio 4: 98–102.

CAMERON, J. N. 1971. Rapid method for determination of total carbon dioxide in small blood samples. J. Appl. Physiol. 31: 632–634.

DILLON, P. J., D. S. JEFFRIES, W. SNYDER, R. REID, N. D. YAN, D. EVANS, J. MOSS, AND W. A. SCHEIDER. 1978. Acidic precipitation in south-central Ontario: recent observations. J. Fish. Res. Board Can. 35: 809–815.

DIVELY, J. L., J. E. MUDGE, W. H. NEFF, AND A. ANTHONY. 1977. Blood pO_2, pCO_2, and pH changes in brook trout (*Salvelinus fontinalis*) exposed to sublethal levels of acidity. Comp. Biochem. Physiol. 57A: 347–351.

DOVLAND, H., E. JORANGER, AND A. SEMB. 1976. Deposition of air pollutants in Norway, p. 14–35. *In* F. H. Braekke [ed.] Impact of acid precipitation on forest and freshwater ecosystems in Norway. SNSF-project FR 6/76.

JANSSEN, R. G., AND D. J. RANDALL. 1975. The effects of changes in pH and pCO_2 in blood and water on breathing in rainbow trout, *Salmo gairdneri*. Respir. Physiol. 25: 235–245.

LIEVESTAD, H., AND I. P. MUNIZ. 1976. Fish kill at low pH in a Norwegian river. Nature 259: 391–392.

LIEVESTAD, H., G. HENDREY, I. P. MUNIZ, AND E. SNEKVIK. 1976. Effects of acid precipitation on freshwater organisms, p. 86–111. *In* F. H. Braekke [ed.] Impact of acid precipitation on forest and freshwater ecosystems in Norway. SNSF-project FR 6/76.

LIKENS, G. E., F. H. BORMANN, AND N. M. JOHNSON. 1972. Acid rain. Environment 14 (2): 33–40.

LLOYD, R., AND D. H. M. JORDAN. 1964. Some factors effecting the resistance of rainbow trout (*Salmo gairdnerii* Richardson) to acid waters. Int. J. Air Water Pollut. 8: 393–403.

LOCKHART, W. L., AND A. LUTZ. 1976. Preliminary biochemical observations of fishes inhabiting an acidified lake in Ontario, Canada. Proc. Ist. Int. Symp. Acid Precip. Forest Ecosystems. *In* special issue J. Water Air Soil Pollut. 545–569.

ODEN, S. 1976. The acidity problem — an outline of concepts. Proc. Ist. Int. Symp. Acid Precip. Forest Ecosystems. *In* special issue J. Water Air Soil Pollut. 1–36.

PACKER, R. K., AND W. A. DUNSON. 1970. Effects of low environmental pH on blood pH and Na^+ balance of brook trout (*Salvelinus fontinalis*). J. Exp. Zool. 174: 65–72.

SMITH, L. S., AND G. R. BELL. 1964. A technique for prolonged blood sampling in free swimming salmon. J. Fish. Res. Board Can. 21: 711–717.

VAALA, S. S., AND R. B. MITCHELL. 1970. Blood oxygen tension changes in acid exposed brook trout. Proc. Pa. Acad. Sci. 44: 41–44.

Myxosoma cerebralis: a Method for Staining Spores and Other Stages with Silver Nitrate

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WOLF, K., AND M. E. MARKIW. 1979. *Myxosoma cerebralis*: a method for staining spores and other stages with silver nitrate. J. Fish. Res. Board Can. 36: 88–89.

Eleven dye substances were tested for their ability to stain *Myxosoma cerebralis* and to be retained through either the pepsin-trypsin-dextrose or the plankton centrifuge method of releasing and concentrating spores. Silver nitrate proved to be the best; it produced a distinctive brown color that has been retained by spores through 2.5 yr of storage. The method has applications in histologic studies of whirling disease, in quantifying the efficiency of spore detection procedures, and in teaching.

Key words: myxosporidans, *Myxosoma cerebralis*, whirling disease, spore staining

WOLF, K., AND M. E. MARKIW. 1979. *Myxosoma cerebralis*: a method for staining spores and other stages with silver nitrate. J. Fish. Res. Board Can. 36: 88–89.

Nous avons essayé onze colorants en vue de déterminer leur aptitude à colorer *Myxosoma cerebralis* et leur rétention lorsque soumis soit à la méthode pepsine-trypsine-dextrose, soit de centrifugation du plancton, pour la mise en liberté et la concentration des spores. Le nitrate d'argent s'avère le meilleur; il produit une coloration brune distinctive retenue par les spores pendant un entreposage de 2,5 mois. La méthode peut être utilisée dans des études histologiques de la maladie giratoire, la quantification de l'efficacité des méthodes de détection des spores et enfin l'enseignement.

Received April 26, 1978
Accepted October 17, 1978

Reçu le 26 avril 1978
Accepté le 17 octobre 1978

SEVERAL procedures have been developed for releasing and concentrating spores of *Myxosoma cerebralis* and thereby facilitating whirling disease diagnostic work, detection, and research applications (Landolt 1973; Markiw and Wolf 1974; O'Grodnick 1975). Considering such factors as purity of final product, the time required for processing, simplicity, and the sensitivity of detection, each method has certain advantages. However, the Fish Health Section of the American Fisheries Society (Anon. 1975) has suggested only two methods for detecting asymptomatic carriers of *M. cerebralis* — the pepsin-trypsin-dextrose (PTD method) of Markiw and Wolf (1974) or the plankton centrifuge method reported by O'Grodnick (1975).

When the number of spores in a pooled sample of fish is low (as in light infections or low incidences) there is some risk of failing to detect the organism — especially if personnel are not well versed in the procedures. Accordingly, we sought a dye substance that would stain spores and persist through either the PTD or plankton centrifuge method of processing, and thereby provide a means of measuring the percentage recovery and hence efficiency.

Printed in Canada (J5224)
Imprimé au Canada (J5224)

Methods — Heads of infected rainbow trout (*Salmo gairdneri*) were immersed for several minutes in water at 50°C, the soft tissues were removed, and the skull and gill arches were minced and then crushed in a mortar and pestle. The resulting material was suspended in water, and the portion that passed through a 125-μm screen was centrifuged at 1200 $\times$ *g* for 10 min. The pelleted tissues fragments and spores were subjected to digestion by pepsin for 60 min and trypsin for 30 min, and then further purified by centrifugation through 55% dextrose. Spores were washed in distilled water and fixed in 5% neutral buffered formalin for 3 or 18 h.

Subsamples of preserved spores were stained with 1 of 11 different biological dye substances (Table 1), subjected to the standard PTD procedure, and examined for color retention and structural integrity.

The efficiency of recovery of stained spores was quantified by seeding known numbers in duplicate portions of finely minced cranial elements and gill arches of healthy rainbow trout fingerlings — each portion equivalent to a pooled sample of 60 fish. The samples were processed by the PTD method, the resulting harvest was brought to the original volume seeded, and the spores were counted in a hemacytometer.

Results and discussion — Silver nitrate proved to be the stain that was retained through PTD processing with little loss of its distinctive yellow to brown colora-

TABLE 1. Biological stains applied to spores of *Myxosoma cerebralis* and tested for persistence through PTD processing[a].

Stain	Concentration (%)	Staining time
Aceto-orcein	1.0	10 min
Crystal violet	1.0	10 min
Crystal violet + Lugol's iodine	1.0	5 min
Hematoxylin-eosin Y (Delafield's)	0.7	4 h
Hematoxylin, iron (Weigert's)	0.5	4 h
Malachite green	1.0	16 h
Methylene blue	1.0	30 min
Osmium tetroxide	1.0	1 h
Pinacyanol	0.25	15 min
Potassium permanganate	1.0	10 min
Silver nitrate	10.0	3 h[b]

[a]Pepsin-trypsin-dextrose centrifugation method of Markiw and Wolf (1974).

[b]After spores were treated with 10% aqueous silver nitrate (pH 4.7) they were exposed to midday sunlight for 2 to 3 h to photo-oxidize the compound.

tion. Aceto-orcein and potassium permanganate were unsatisfactory because they damaged spores. Although they stained spores well, crystal violet, malachite green, and methylene blue pigments were lost during PTD processing. Osmium tetroxide did not stain adequately. The hematoxylin stains and pinacyanol imparted good pigmentation, but their retention was less than that of silver nitrate.

Spores stained with silver nitrate were preserved at 4°C in a 12.5% solution of polyvinylpyrrolidone (M.W. 40,000), 5% formalin, or water. The least loss of pigment occurred in water; polyvinylpyrrolidone was wholly unsatisfactory (Fig. 1). In spite of the small size of the spores, a 3-h fixation time in formalin before staining with silver nitrate was inadequate. Periodic counts of stained spores held in water after a 16-h fixation in formalin showed that spore numbers were stable for at least 2.5 yr.

As a result of impregnation with silver nitrate and later exposure to sunlight at midday, spore valves were stained a yellowish brown and the polar capsules or the extruded filaments an intense brown. Pre-spore stages were stained like the valves, and presumptively identified trophozoites were amorphous masses showing multiple brown pigment spots. Because of differential avidity for the silver compound, histologic sections of fish tissue with *M. cerebralis* showed the parasite in marked contrast to surrounding host cells.

Minced normal trout bone and cartilage was seeded with silver stained spores at rates of from 1000 to 2000 per head. In eight trials, the average recovery was 91% of the number seeded (range, 67–131%).

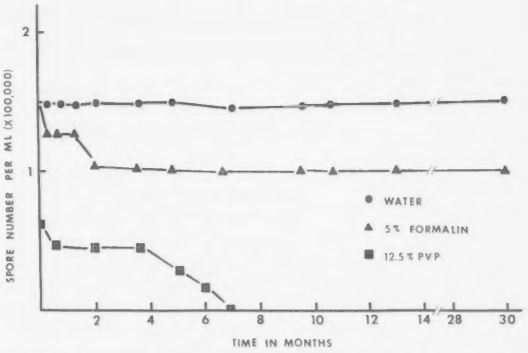

FIG. 1. Comparison of intact survival of *M. cerebralis* spores stained with silver nitrate and held in water, 5% formalin, or 12.5% solution of polyvinylpyrrolidone (PVP).

We suggest that silver stained spores be used to measure the efficiency of recovery when critical detection is required, or when persons first use either the PTD or the plankton centrifuge method. However, the stained spores should be used in a separate but parallel mince of normal tissue and not with the unknown, for about 7% of the spores blanched to a pale yellow color. The inexperienced investigator might confuse the lightly stained spores with untreated spores and report a false positive.

Judging by our work with stained spores, a few spores can and often do adhere to plankton centrifuge walls or rotor, or to blenders, food choppers, and laboratory ware. Presumably, unstained spores can similarly adhere to walls of utensils and conceivably could give rise to a false positive in later work. Soaking such equipment for 30 min in household bleach diluted with an equal volume of water is sufficient to dissolve or otherwise decontaminate the utensils.

ANON. 1975. Suggested procedures for the detection and identification of certain infectious diseases of fishes. Fish Health Section, American Fisheries Society. U.S. Fish Wildl. Serv., Washington, D.C. 90 p.

LANDOLT, M. L. 1973. *Myxosoma cerebralis*: isolation and concentration from fish skeletal elements — trypsin digestion method. J. Fish. Res. Board Can. 30: 1713–1716.

MARKIW, M. E., AND K. WOLF. 1974. *Myxosoma cerebralis*: isolation and concentration from fish skeletal elements — sequential enzymatic digestions and purification by differential centrifugation. J. Fish. Res. Board Can. 31: 15–20.

O'GRODNICK, J. J. 1975. Whirling disease *Myxosoma cerebralis* spore concentration using continuous plankton centrifuge. J. Wildl. Dis. 11: 54–57.

Precocious Sexual Development in Hatchery-Reared and Laboratory-Maintained Male Steelhead Trout (*Salmo gairdneri*)

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SCHMIDT, S. P., AND E. W. HOUSE. 1979. Precocious sexual development in hatchery-reared and laboratory-maintained male steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 36: 90–93.

The incidence of precocious steelhead trout (*Salmo gairdneri*) was determined in several Idaho hatchery steelhead populations. The range of incidence of precocious males was 0–64% of the sampled populations. This variation appeared to be related to age of the trout, water temperature, and photoperiod. The incidence of precocious males greatly exceeded the incidence (0.1% of the population when encountered) of precocious females. Precocious male steelhead trout are apparently lost from the migrating smolt population and display mating behavior similar to sea-run adult male steelhead. Precocious males maintained in laboratory conditions remained sexually mature for at least 6 mo of observation. This was reflected by mean gonadal weights and mean gonadosomatic indices from precocious male steelhead which differed significantly from nonprecocious juvenile male steelhead maintained under similar conditions. No consistent pattern of growth was observed among laboratory-maintained trout.

Key words: steelhead trout, reproduction, precocious sexual maturation, age, photoperiod, temperature

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Nous avons déterminé l'occurrence de truites steelhead (*Salmo gairdneri*) précoces dans plusieurs populations de steelhead de l'Idaho d'élevage. La gamme d'occurrence de mâles précoces s'étend de 0 à 64% des populations échantillonnées. Cette variation semble liée à l'âge des truites, à la température de l'eau et à la photopériode. L'occurrence des mâles précoces dépasse de beaucoup celle (0,1% de la population, lorsque présentes) des femelles précoces. Il semble que les truites steelhead mâles précoces se détachent de la population de smolts migrateurs et exhibent un comportement reproducteur semblable à celui de truites steelhead mâles anadromes. Les mâles précoces maintenus dans des conditions de laboratoire sont demeurés sexuellement matures durant au moins 6 mois d'observation. C'est ce qu'indiquent le poids moyen des gonades et les indices gonado-somatiques moyens de truites steelhead mâles précoces, dont les valeurs diffèrent de façon significative de celles de jeunes truites steelhead non précoces maintenues dans des conditions semblables. Nous n'avons observé aucun mode de croissance uniforme chez les truites maintenues en laboratoire.

Received January 10, 1978
Accepted October 11, 1978

Reçu le 10 janvier 1978
Accepté le 11 octobre 1978

EXPERIMENTAL and descriptive studies of precocious sexual development in the male pink salmon (*Oncorhynchus gorbuscha*) have been reported (MacKinnon and Donaldson 1976; Funk and Donaldson 1972a, 1972b; Donaldson et al. 1972). Robertson (1957) and Gebhards (1960) have documented the life history and spawning survival of precocious male chinook salmon (*O. tshawytscha*). Saunders and Henderson (1965) have described laboratory-reared Atlantic salmon (*Salmo salar*) males that were sexually mature as postsmolts and Lee and Power (1976) have discussed the possible significance of precocious male Atlantic salmon of the Leaf River, Ungava Bay, Canada. Precocious sexual development among steelhead trout (*S. gairdneri*) has been mentioned by several authors (Zaugg and McLain 1972; Robertson and Wexler 1960). McKenzie et al. (1978) noted the existence of precociously mature male steelhead in one Idaho steelhead hatchery. To our knowledge, however, no reports that exclusively discuss precocity in steelhead trout exist in the literature.

Materials and methods — Precocious male and female steelhead were identified from nonprecocious developing smolts in hatchery populations after anesthetization in MS-222®. Milt or eggs could be stripped from the precocious steelhead trout at the time of collection. The external ap-

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Printed in Canada (J5092)
Imprimé au Canada (J5092)

pearance of the precocious steelhead was characterized by retention of parr markings and a brilliant coloration reminiscent of mature adult spawning steelhead which stood in sharp contrast to the silvery appearance of developing smolts.

The incidence of precocious steelhead trout males in hatchery populations at three Idaho Fish and Game Department Hatcheries was determined. Precocious males were identified in the rearing ponds at the Hayden Creek Research Station near Lemhi, Idaho, on March 27, 1975. A second collecting trip was conducted May 18, 1975 to the Hayden Creek facility, approximately 6 wk following the release of the juvenile steelhead population from the rearing ponds into Hayden Creek. On this trip precocious males were identified near the adult steelhead spawning areas at the Hayden Creek Station.

Estimates of the occurrence of precocious males in the population of juvenile steelhead at the Niagara Springs Hatchery near Wendell, Idaho, were obtained during March and early April of 1976. Steelhead from this hatchery are transported to the Pahsimeroi River Steelhead Hatchery near May, Idaho, for release into the Salmon River drainage. In late April, precocious male steelhead were identified at this location following the release of the Niagara Springs reared steelhead. From this population of fish, precocious males and nonprecocious juvenile steelhead were transported to Idaho State University where they were maintained in wooden epoxy-sealed aquaria. The water temperature in the aquaria was maintained between 8° and 10°C. The photoperiod within the fish-holding laboratory was manipulated to simulate that of natural environmental conditions. The fish were fed daily with Purina Trout Chow.

From June 1976 through December 1976 five precocious male steelhead and five nonprecocious trout were killed monthly by over anesthetization in MS-222®. Each fish was weighed to the nearest milligram, the standard length was recorded, and the gonads were removed and fixed in Baker's 10% Formalin. Following fixation, the gonads were weighed to the nearest 0.1 g and a gonadosomatic index (GSI) was determined for each fish from the equation

$$\text{GSI} = \text{weight of gonads} \times 100/\text{body wt}$$

Further estimates of the incidence of precocious males in the Niagara Springs reared–Pahsimeroi River released steelhead population were obtained in the Spring of 1977. In March 1977 the population of steelhead at the Niagara Springs Hatchery was examined. In April and May precocious males were identified at the Pahsimeroi River facility.

One precocious female steelhead trout was identified at the Hayden Creek rearing pond on March 27, 1975, and one precocious female was identified from the April 6, 1976 sampling at the Niagara Springs rearing raceway. Precocious females were not present in any of the other samples.

Results and discussion — Table 1 shows the percentage of precocious steelhead in the sampled hatchery populations. Early gonad ripening in hatchery-reared steelhead populations was first observed in March when 10% of the fish that had been maintained for 2 yr at the Hayden Creek Steelhead Hatchery were precocious males. In contrast, among 1-yr-old fish at the Niagara Springs Steelhead Hatchery, no precocious males were identified on March 18, 1976 and only 0.25% in March the following year. In April 1976 the incidence of precocity had risen to 18% at the Niagara Springs Hatchery. Because all other environmental variables remained constant, increasing photoperiod probably triggered the sexual maturation.

TABLE 1. Percentage of precociously mature steelhead trout from hatchery-sampled populations in Idaho.

Sampling date	Location	Precocious males (%)	Precocious females (%)
Mar. 27, 1975	Hayden Creek Rearing Ponds	10	0.1
May 18, 1975	Hayden Creek Spawning Areas	50	0
Mar. 18, 1976	Niagara Springs Rearing Raceways	0	0
Apr. 6, 1976	Niagara Springs Rearing Raceways	18	0.1
Apr. 28, 1976	Pahsimeroi River Hatchery	32	0
Mar. 26, 1977	Niagara Springs Rearing Raceways	0.25	0
Apr. 29, 1977	Pahsimeroi River Hatchery	36	0
May 24, 1977	Pahsimeroi River Hatchery	64	0

Following the release of the hatchery populations into their home streams the incidence of precocious males remaining on or near the adult spawning grounds was high. Upon the arrival of sea-run females, the precocious males were observed to attend the females as do sea-run males. Do these males produce viable spermatozoa? We have observed active spermatozoa microscopically and personnel of the Idaho Fish and Game Department have fertilized sea-run female eggs with precocial male milt. It is unlikely, however, with the present Idaho Fish and Game Department hatchery propagation methods that precocious male steelhead fertilize adult female eggs.

The precocious males apparently remain in the home streams and are lost from the migrating smolt population. Evropeitseva (1960) has suggested that precocious male *Salmo salar* do not migrate seaward. Precocious males collected in previous years and maintained in our laboratory had high mortality rates in June and July which suggests that precocious males remaining in streams may die. This may constitute a significant loss to the numbers of fish for sport and commercial fishing. In contrast, Funk and Donaldson (1972b) reported that immature pink salmon induced to precocious sexual maturation following salmon gonadotropin injections did not die after reaching maturity. In addition, Robertson (1957) reported that artificially spawned precocious male chinook salmon survived and exhibited renewed spermatogenesis 5 mo following spawning.

Temperature may play an important role in the induction of precocity. MacKinnon and Donaldson (1976) have demonstrated a relationship between

TABLE 2. Mean (± SE) body weight, standard length, gonad weight, and gonadosomatic index (GSI) of precocious male and nonprecocious male juvenile steelhead trout (*Salmo gairdneri*) maintained in the laboratory and measured at monthly intervals. $n = 5$ for each group.

	Group	Body wt (g)	Standard length (cm)	Gonad wt (g)	GSI
June	Precocious	139.2±22.1	21.1±1.2	4.01±1.05	2.92±0.61
	Nonprecocious	78.5±8.9	17.0±0.9	0.66±0.37**	0.10±0.07**
July	Precocious	124.0±14.9	21.1±1.1	2.25±0.30	1.94±0.37
	Nonprecocious	92.6±5.3	19.2±0.5	0.10±0.02**	0.11±0.02**
Aug.	Precocious	111.5±15.4	19.7±0.9	1.86±0.17	1.77±0.22
	Nonprecocious	79.7±10.0	17.2±0.9	0.24±0.14**	0.26±0.13**
Sept.	Precocious	131.0±16.2	20.8±1.0	3.64±0.60	2.76±0.31
	Nonprecocious	101.8±23.5	19.9±2.3	0.24±0.04**	0.24±0.00**
Oct.	Precocious	126.0±16.1	21.1±0.9	2.92±0.71	2.07±0.27
	Nonprecocious	63.2±2.1*	16.8±0.4*	0.06±0.03**	0.09±0.03**
Nov.	Precocious	127.5±7.8	21.1±0.3	3.56±0.43	2.77±0.20
	Nonprecocious	68.6±2.2*	17.4±0.1*	0.02±0.01**	0.03±0.01**
Dec.	Precocious	161.7±26.7	22.2±1.2	4.04±1.31	2.33±0.25
	Nonprecocious	58.5±8.5*	17.4±1.5*	0.02±0.00**	0.04±0.00**

*Significant difference between means (t-test, $P < 0.05$). **Highly significant difference between means (t-test, $P < 0.01$).

elevated water temperature and the incidence of precocity among pink salmon males. The water temperature at the Niagara Springs facility remains constant at 15°C whereas the temperature of the water at the Hayden Creek facility may drop as low as 4°–5°C in early Spring. Precocious male steelhead were identified in 4°C water at the Hayden Creek facility in March 1975 but these fish were 1 yr older than the Niagara Springs reared steelhead. In addition, the number of precocious males among the 1-yr-old fish at Niagara Springs sampled in April from the rearing raceways was high. These data suggest that elevated water temperature may increase the incidence of precocious males. However, genetic differences between these hatchery stocks dictating different growth rates could contribute to this phenomenon.

That precocity is not expressed until March in steelhead trout suggests an involvement of increasing photoperiod in this process. MacKinnon and Donaldson (1976) have indicated the probable importance of photoperiod in stimulating maturation in the pink salmon. Hoffman (1970) has reviewed the role of the epiphyseal complex in fish in mediating the effect of changing photoperiod upon reproductive maturation. In some fishes Fenwick (1970) reports that melatonin, an epiphyseal secretion, appears to exert an inhibitory effect upon gonadal function. Preliminary investigations in our laboratory revealed significant differences in epiphyseal weights of precocious steelhead males compared to nonprecocious males.

Only two precociously mature female steelhead were identified on the collecting trips. Their coloration was similar to that described for precocious males. It was possible to strip eggs from them by stroking the abdomen of the fish anteroposteriorally. The low incidence of precocity in female steelhead trout may be due to a sex-linked genetic phenomenon. Funk and Donaldson (1972a) were unable to induce an equivalent level of precocious sexual development in female pink salmon injected with salmon gonadotropin as that obtained in males.

Table 2 shows that laboratory-maintained precocious males had mean body weights and mean standard lengths that exceeded those of nonprecocious males over a 7-mo period. These differences were significantly different (t-test, $P < 0.05$) in October, November, and December. There was no consistent growth pattern among either precocious or nonprecocious steelhead maintained in the laboratory. MacKinnon and Donaldson (1976) suggested that in pink salmon a critical size must be obtained before the initiation of gonadal development. This factor may also be important in steelhead trout but a larger sample size is necessary to reveal it.

Gonadal hypertrophy was observed in all precocious males maintained in the laboratory with the testes occupying a large portion of the body cavity. This sexual maturity was reflected by precocious male mean gonadal weights and GSI which were considerably greater (t-test, $P < 0.01$) than nonprecocious males throughout the study (Table 2). The precocious males were classified in either category number 4 or 5 of the Funk and Donaldson (1972b) classification of sexual maturity of the testis for pink salmon. Milt could be stripped from the fish (category 5) by stroking the abdomen in an anteroposterior direction in 100%

of the precocious fish examined in all months except July, September, and October. In these latter months there was an apparent regression of 20% of the precocious males to category 4 as the fish displayed extreme gonadal hypertrophy but milt could not be stripped. The remaining 80% of the sampled precocious males during these months were classified in category 5.

Acknowledgments — We gratefully acknowledge the assistance of the following Idaho Fish and Game Department personnel: S. Gebhards, M. Reingold, D. Anderson, R. Quidor, T. Levendofske, and V. Moore.

DONALDSON, E. M., J. D. FUNK, F. C. WITHLER, AND R. B. MORLEY. 1972. Successful fertilization of pink salmon (*Oncorhynchus gorbuscha*) ova by spermatozoa from gonadotropin-injected juvenile pink salmon. J. Fish. Res. Board Can. 29: 13–18.

EVROPEITSEVA, N. V. 1960. Soolnoshenie protsessov rannego razvitiia gonad i perekhod v pokatnoe sostoianie u samtsov Baltiiskoyo lososia (*Salmo salar* L.) v prudovykh usloviiakh. [Correlation between the processes of early gonad ripening and transformation to the seaward-migrating stage among male Baltic salmon (*Salmo salar* L.) held in ponds.]. Zool. Zh. 39: 777–779.

FENWICK, J. C. 1970. Demonstration and effect of melatonin in fish. Gen. Comp. Endocrino. 14: 86–97.

FUNK, J. D., AND E. M. DONALDSON. 1972a. Induction of precocious sexual development in female pink salmon (*Oncorhynchus gorbuscha*). Can. J. Zool. 51: 493–500.

1972b. Induction of precocious sexual maturity in male pink salmon (*Oncorhynchus gorbuscha*). Can. J. Zool. 50: 1413–1419.

GEBHARDS, S. V. 1960. Biological notes on precocious male chinook salmon parr in the Salmon River drainage, Idaho. Prog. Fish Cult. 22: 121–123.

HOFFMAN, R. A. 1970. The epiphyseal complex in fish and reptiles. Am. Zool. 10: 191–199.

LEE, R. L. G., AND G. POWER. 1976. Atlantic salmon (*Salmo salar*) of the Leaf River, Ungava Bay. J. Fish. Res. Board Can. 33: 2616–2621.

MACKINNON, C. N., AND E. M. DONALDSON. 1976. Environmentally induced precocious sexual development in the male pink salmon (*Oncorhynchus gorbuscha*). J. Fish. Res. Board Can. 33: 2602–2605.

MCKENZIE, J. E., E. W. HOUSE, J. G. MCWILLIAM, AND D. W. JOHNSON. 1978. Coronary degeneration in sexually mature rainbow and steelhead trout, *Salmo gairdneri*. Atherosclerosis 29: 431–437.

ROBERTSON, O. H. 1957. Survival of precociously mature king salmon male parr (*Oncorhynchus tshawytscha*) after spawning. Calif. Fish Game Dep. Bull. 43: 119–130.

ROBERTSON, O. H., AND B. C. WEXLER. 1960. Hyperplasia of the adrenal cortical tissue in Pacific salmon (genus *Oncorhynchus*) and rainbow trout (*Salmo gairdneri*) accompanying sexual maturation and spawning. Endocrinology 65: 225–238.

SAUNDERS, R. L., AND E. B. HENDERSON. 1965. Precocious sexual development in male post-smolt Atlantic salmon reared in the laboratory. J. Fish. Res. Board Can. 22: 1567–1570.

ZAUGG, W. S., AND L. R. MCLAIN. 1972. Changes in gill adenosine-triphosphatase activity associated with parr–smolt transformation in steelhead trout, coho, and spring chinook salmon. J. Fish. Res. Board Can. 29: 167–171.

Survival and Growth of Juvenile American Lobsters (*Homarus americanus*) After Eyestalk Ablation

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The effect of size at the time of ablation on postoperative survival was assessed by removing the eyestalk from 4th, 5th, and 6th stage juvenile American lobsters (*Homarus americanus*) 6 d postmolt. The 6th stage juveniles exhibited significantly higher survival (72.8%) through three postoperative molts than the 5th or 4th stage lobsters (45 and 30% survival, respectively). Survival of control lobsters through the same number of molts was 90%. The feeding of a nutritionally adequate diet (frozen brine shrimp) was of prime importance with regard to survival of both ablated and control lobsters. The mean percent total weight gains for these three postablation molts were 610, 571, and 642% for 4th, 5th, and 6th stage lobsters, respectively, while the weight gain for control

Printed in Canada (J5156)
Imprimé au Canada (J5156)

lobsters was 407%. The data suggest that eyestalk ablation should not be performed earlier than 6th stage for maximum survival and growth.

Key words: eyestalk ablation, American lobster, survival, growth

TRIDER, D. J., E. G. MASON, AND J. D. CASTELL. 1979. Survival and growth of juvenile American lobsters (*Homarus americanus*) after eyestalk ablation. J. Fish. Res. Board Can. 36: 93–97.

Nous avons mesuré l'effet de la taille au moment de l'ablation sur la survie des homards après l'opération, en enlevant le pédoncule oculaire de jeunes homards (*Homarus americanus*) de 4e, 5e et 6e stades six jours après la mue. Les jeunes de 6e stade ont une survie nettement plus élevée (72,8%) au cours de trois mues postopératoires que les homards aux 5e ou 4e stades (survie de 45% et de 30% respectivement). La survie des témoins durant un même nombre de mues est de 90%. La survie, tant des homards opérés que des témoins, dépend beaucoup d'un régime alimentaire adéquat (artemies congelées). Les gains pondéraux totaux, en pourcentage, durant ces trois mues postopératoires sont de 610, 571 et 642% pour des homards de 4e, 5e et 6e stades respectivement, alors que le gain pondéral des témoins est de 407%. Ces données donnent à croire que l'ablation du pédoncule oculaire ne devrait pas se faire avant le 6e stade si l'on veut obtenir un maximum de survie et de croissance.

Received February 16, 1978
Accepted September 15, 1978

Reçu le 16 février 1978
Accepté le 15 septembre 1978

THERE is a long history of eyestalk ablation research with crustaceans dating back to before the turn of the century. Until recently eyestalk ablation of crustaceans was always associated with high mortality. The ablated animal usually died before or during the first postoperative molt (Abramowitz and Abramowitz 1940). Few ever survived beyond the third postoperative molt (See review by Passano 1960). Smith (1940) had suggested that feed might be playing an important role in the high mortality of ablated crustaceans. It seemed logical that if eyestalk ablation increased the growth rate, it would also increase the food requirement. Mauviot and Castell (1976), by feeding adequate diets, were able to obtain up to nine postoperative molts with eyestalk ablated juvenile American lobsters (*Homarus americanus*). They also demonstrated (Castell et al. 1976) that the quality as well as the quantity of food was very critical to the survival of juvenile lobsters. Castell et al. (1977) also found that good diets promoted high survival of larger (200–300 g) commercially caught lobsters after they were ablated.

In all this recent work with lobsters the growth acceleration of the ablated lobsters was dramatic and continued through each successive postoperative molt. In growing lobsters from the egg to market size in a commercial culture system, the earlier one could perform eyestalk ablations, the sooner one would have market size lobsters. One of the limiting factors in establishing commercial lobster farming is the long time it takes for lobsters to grow from egg to market size. The objective of the present research report was to determine the earliest size at which eyestalk ablations could be performed on lobsters.

Materials and methods — Lobster larvae were hatched and reared to 4th stage as described by Mauviot and Castell (1976). The 4th stage juveniles were placed in trays with individual compartments in 20°C, filtered seawater (32 g/L). These animals were fed ad lib. each day with frozen adult brine shrimp (San Francisco Bay brine shrimp).

Eyestalks were removed from 25, 4th stage lobsters 6 d postmolt. The eyestalks were severed at the base using a 26-gauge hypodermic needle as a lance. This procedure was later repeated on 23, 5th stage and 24, 6th stage lobsters from the same hatch using a 20-gauge needle. There were five, three, and two postoperative deaths in the 4th, 5th, and 6th stage groups, respectively. A group of 40 intact animals from the same hatch served as controls. A second group of 4th stage lobsters and 20 control animals from another hatch were also tested. This ablated group had approximately 20% postoperative mortality as well.

Lobsters were checked daily for molts and mortalities. Animals were weighed every 2 wk. Intermolt period and weight gain of ablated animals were compared to controls using a *t*-test. The growth curves for each group were determined by regression analysis of the $\log_{10}$ of the weight against time.

Although the experiment was terminated after each group of ablated lobsters had completed three postoperative molts, three lobsters were retained to see how long they could survive after ablation.

Results — The age (stage) or size of juvenile lobsters at the time of eyestalk ablation has proved to have a definite effect on postoperative survival. Lobsters ablated while in the 4th or 5th stage suffered heavy mortalities (Table 1). The majority of these mortalities occurred not during the first postoperative molt, but during or shortly after the second molt. Lobsters ablated in the 6th stage experienced a relatively low (22.7%) mortality during the first postoperative molt with good survival through the next two molts. Initial mortalities (10%) in control group "A" were associated with a

TABLE 1. Total percent survival of control and ablated lobsters at each molt period.

	Molt period				
	4–5	5–6	6–7	7–8	8–9
Control A	90	90	90	90	82.5
4th A	100[a]	75	30	—[b]	
5th A		100[a]	90	45	—[b]
6th A			77.3[a]	77.3	72.7
Control B	100	100	95	90	90
4th B	90[a]	70	35	—[b]	

[a]Eyestalk ablated.
[b]Experiment terminated.

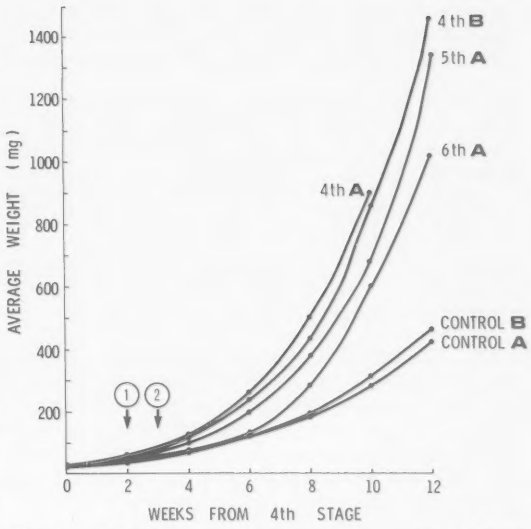

FIG. 1. Growth curves of ablated and control lobsters from 4th stage to termination. ① Indicates when 5th stage animals were ablated; ② indicates when 6th stage animals were ablated.

fungal infection similar to that described by Nilson et al. (1976). The holding facility was disinfected with iodophor and no further outbreaks of fungal infections were observed in any of the lobsters.

As has been previously demonstrated (Mauviot and Castell 1976), ablated lobsters in this study had shorter intermolt periods than control animals (Table 2). The intermolt period increased with each successive molt for all animals as was noted by Mauviot and Castell (1976). The length of common intermolt periods was not affected by the stage at which the ablation was performed. The intermolt period from 6th to 7th stage was approximately 12 d for all groups of ablated lobsters (Table 2).

The total percent weight gains after three post-operative molts were 610, 571, and 642% for lobsters ablated at 4th, 5th, and 6th stages, respectively, compared with 407% weight gain for control group "A" lobsters. The average percent weight gains for ablated and control lobsters are given in Table 3. No significant differences were seen among lobsters of ablated groups during common molt periods. The actual growth of each group of lobsters is best illustrated in Fig. 1 which shows average weight vs. time. No significant differences were seen between the two 4th stage ablated groups. This was also true of the two control groups up to the 8th week.

The best fit curves for the weight gain data shown in Fig. 1 were exponentials of the form

$$\omega = \omega_0 \times 10^{bt}$$

where ω = weight at time t in weeks, ω_0 = initial weight, and b = growth rate constant. The growth rate constant b was 0.10 for the control groups, 0.14 for both groups ablated at 4th stage and also those ablated at the 5th stage. The growth rate constant for the 6th stage ablated lobsters was 0.16, suggesting that although these animals 12 wk after 4th stage were smaller than lobsters ablated at earlier stages, they would eventually surpass the other groups in size. The correlation coefficients for the logarithmic regression analysis of growth data were all very good ranging from 0.86 to 0.99.

Fourteen months after hatching and about 13 mo after ablation, two of the three retained ablated lobsters were still alive. The third died of a suspected "gas-

TABLE 2. Average intermolt period in days (± SD) of ablated and control lobsters (numbers in parentheses indicate number of obsters tested). (*Significantly different from control animals.)

	Molt interval (days)				
	4–5	5–6	6–7	7–8	8–9
Control A	14.5±1.8 (36)	14.4±2.1 (36)	17.75±2.0 (36)	18.1±2.9 (36)	20.3±2.8 (33)
4th A	11.3±0.66 (20)*	10.1±1.4 (15)*	12.8±0.75 (6)*	—	—
5th A	14.8±2.1 (20)	11.0±1.0 (20)*	11.9±2.0 (18)*	15.4±3.7 (11)*	—
6th A	15.7±1.9 (22)	15.2±1.7 (22)	12.2±1.3 (17)*	12.82±1.3 (17)	15.1±1.3 (16)
Control B	15.5±2.2 (20)	13.7±2.6 (19)	16.4±2.9 (18)	18.05±2.1 (18)	20.05±3.9 (18)
4th B	10.9±0.8 (18)*	10.75±0.75 (14)*	13.85±1.95 (7)*	—	—

TABLE 3. Average percent weight gain per molt of ablated and control lobsters (± SD). (*Significantly different from control group at this time.)

	Molt period				
	4–5	5–6	6–7	7–8	8–9
Control A	59.8±22.2	78.3±14.6	77.9±12.2	62.1±14.4	54.5±8.8
4th A	95.3±15.4*	78.8±14.6	103.3±18.1*	—	—
5th A	—	86.3±26.6	91.1±16.6*	88.6±13.4*	—
6th A	—	—	87.8±16.8*	94.6±10.6*	103.1±13.9*
Control B	63.5±12.4	75.9±19.2	88.0±11.5	78.4±9.2	62.4±5.6
4th B	86.0±17.3*	107.6±14.9*	92.9±15.5	—	—

bubble disease" 13 molts after ablation at 6th stage. The two survivors (one ablated at 4th stage and one at 6th stage) successfully completed 22 molts each and attained "canner" size or larger before they perished. Again gas-bubble disease was suspected. These animals had been fed fresh clams and crabs alternated with frozen squid and shrimp.

Discussion — The high mortality observed in the 4th stage group prompted the ablation of a second group of 4th stage juveniles as a check on the ablation technique and survival. Results from this second group confirmed the high mortality of lobsters ablated at this stage. This indicated that the 4th stage lobsters were not able to cope with the stress of eyestalk ablation even with the feeding of an adequate diet. Rao et al. (1973) reported similarly high mortalities (75%) after only two postoperative molts with 4th stage lobsters. This high mortality at an earlier molt may be the result of feeding a deficient diet (guppy food) or starvation. The importance of nutrition and feeding of eyestalk ablated lobsters has been demonstrated (Mauviot and Castell 1976; Castell et al. 1976). The very small size of 4th stage lobsters might have made the operations more difficult and thus contributed to the high mortality. This did not appear to be the case in the present experiment. The operations were made simple and efficient by using a small gauge hypodermic needle and a magnifying glass. The fact that the second postoperative molt proved to be the most critical point in the 4th and 5th stage groups suggested that deaths were a result of some factor other than operative shock, rough handling, starvation, or nutritional deficiency. Perhaps in the transition from a pelagic to a benthic animal (Hughes and Matthiessen 1962), 4th to 6th stage, there are physiological changes occurring that may stress the animals to the point where the additional shock of eyestalk ablation is not well tolerated. Once the lobster reaches 6th stage, it appears to be a stronger animal that is able to cope with the induced physiological changes of eyestalk ablation provided a suitable diet is fed. Nutrition appears to be a key factor beyond the 3rd postoperative molt after ablation at the 6th stage. Whatever the explanation may be, the present results show a definite relationship between the stage when eyestalks are removed and resultant survival.

The average weight gains show ablated animals were growing at a faster rate. This is not due to just water uptake but also to tissue systhesis as demonstrated by Mauviot and Castell (1976) and Castell et al. (1977). They found that the "percent" protein, dry weight, and edible meat were the same for both ablated and control animals even though the former were larger. Initial growth is due to water uptake at molt with subsequent tissue synthesis during the intermolt period.

Considering the good survival of the 6th stage juveniles, we should try to raise significant numbers (100 or more) of ablated lobsters from 6th stage through to market size. This could be accomplished in approximately 1½ yr provided the animals are fed a nutritionally adequate diet (in suitable quantity) and the water quality closely monitored. These are key factors since ablated lobsters are more susceptible to dietary deficiencies and changes in water quality (Castell et al. 1976).

Acknowledgments — We thank Drs D. E. Aiken and D. W. McLeese of the St. Andrew's Biological Station and Drs M. Gilgan and M. F. Li of the Halifax Laboratory for their helpful comments in the preparation of this manuscript.

ABRAMOWITZ, R. K., AND A. A. ABRAMOWITZ. 1940. Molting, growth and survival after eyestalk removal in *Uca pugilator*. Biol. Bull. 78: 179–188.

CASTELL, J. D., J. F. COVEY, D. E. AIKEN, AND S. L. WADDY. 1977. The potential for eyestalk ablation as a technique for accelerating growth of lobsters (*Homarus americanus*) for commercial culture. Proc. Annu. Meet. World Maricult. Soc. 8: 895–914.

CASTELL, J. D., J. C. MAUVIOT, AND J. F. COVEY. 1976. The use of eyestalk ablation in nutrition studies with American lobsters (*Homarus americanus*). Proc. Annu. Meet. World Maricult. Soc. 7: 431–441.

HUGHES, J. T., AND G. C. MATTHIESSEN. 1962. Observations on the biology of the American lobster, *Homarus americanus*. Limnol. Oceanogr. 7: 414–421.

MAUVIOT, J. C., AND J. D. CASTELL. 1976. Molt and growth enhancing effects of bilateral eyestalk ablation on juvenile and adult American lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 33: 1922–1929.

NILSON, E. H., W. S. FISHER, AND R. A. SHLESER. 1976. A new mycosis of larval lobster (*Homarus americanus*). J. Invertebr. Pathol. 27: 177–183.

PASSANO, L. M. 1960. Molting and its control, p. 473–536. *In* T. H. Waterman [ed.] The physiology of Crustacea. Academic Press, Inc., New York, N.Y.

RAO, K. R., S. W. FINGERMAN, AND M. FINGERMAN. 1973. Effects of exogenous ecdysones on the molt cycles of fourth and fifth stage American lobsters (*Homarus americanus*). Comp. Biochem. Physiol. 44A: 1105–1120.

SMITH, R. I. 1940. Studies on the effects of eyestalk removal upon young crayfish *Cambarus clarkii* (Girard). Biol. Bull. 79: 145–152.

Maybe You Can't Get There from Here[1]: A Foreshortened History of Research in Relation to Management of Pacific Salmon

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LARKIN, P. A. 1979. Maybe you can't get there from here: a foreshortened history of research in relation to management of Pacific salmon. J. Fish. Res. Board Can. 36: 98–106.

The standard religion of Pacific salmon research and management was developed by the 1930s and persists today: that adequate husbandry of the resource requires research on the biology of salmon, regulation to ensure sustained yield, protection of the environment to ensure the means of production, and enhancement measures to augment natural production and to mitigate effects of imperfect regulation and protection. Through the 1930s into the 1950s, there were substantial gains in understanding the biology of salmon and relating it to management. Salmon cultural techniques fell into disrepute. In the 1950s and 1960s, the pressures of other resource uses and international conventions greatly expanded perceptions of management and stimulated major discoveries about salmon biology. Economists began to seriously examine the salmon fisheries and perceived the need for limited entry. By the late 1960s the salmon fishery had become highly complex and there was a resurrection of the erstwhile hopes for salmon culture as an integral part of management. Planning exercises for the Salmonid Enhancement Program underlined that integration into a total system of management was crucial to success.

For the future, for salmon to be doubled in abundance rather than halved, the manager's perspective must be more closely identified with that of salmon. In addition to the continuing needs for protection of environment and a broadly balanced enhancement program with an appropriate amount of research and evaluation, there are some necessary changes in attitude concerning regulation. Under *no* circumstances should the permissible harvest of any race of salmon be exceeded. Day-to-day regulation should be geared to salmon biology, not human convenience. Experimental regimes of regulation should be undertaken with suitable commitment to long-term research. Unless such measures are taken, it is realistic to speculate that "maybe we can't get there from here."

Key words: Pacific salmon, resource management, salmonid enhancement

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Le credo auquel on adhère encore aujourd'hui pour la recherche et la gestion des saumons du Pacifique a été élaboré au cours des années 1930 : l'exploitation rationnelle de la ressource comporte des recherches sur la biologie des saumons, la réglementation en vue d'un rendement soutenu, la protection de l'environnement pour la sauvegarde des moyens de production et enfin la mise en valeur visant à augmenter la production naturelle et atténuer les effets d'une réglementation et d'une protection imparfaites. Entre les années 1930 et 1950, on acquit beaucoup de connaissances sur la biologie et on fit des progrès dans l'application de ces connaissances à la gestion des stocks. La pisciculture et ses techniques perdirent de leur popularité. Pendant les années 1950 et 1960, l'importance de la gestion se fit davantage sentir à la suite des pressions résultant d'usages plus nombreux de la ressource et des conventions internationales. Ceci entraîna d'importantes découvertes sur la biologie des saumons. Les économistes commencèrent à examiner sérieusement les pêcheries de saumons et à réaliser la nécessité de limiter le nombre de nouveaux venus. A la fin des années 1960, la pêche des saumons était devenue fort complexe

[1]Fry Lecture, delivered to the Annual Meeting of the Canadian Society of Zoologists, May 17, 1978, London, Ont.

Printed in Canada (J5262)
Imprimé au Canada (J5262)

et l'on vit ressusciter les espoirs de jadis d'une pisciculture qui serait partie intégrale de la gestion. Lors de la planification du Programme de mise en valeur des salmonidés, on a souligné l'importance capitale d'une intégration en un système de gestion total pour le succès de l'entreprise.

Pour l'avenir, si l'on veut doubler plutôt que réduire de moitié l'abondance des saumons, il faudra que la perspective du gestionnaire s'identifie davantage avec celle du saumon. Il faudra toujours protéger l'environnement et poursuivre un programme de mise en valeur bien étayé par la recherche et l'évaluation. Mais en plus, il faudra modifier certaines attitudes vis-à-vis la réglementation. En *aucune* circonstance devrait-on permettre de capturer plus de saumons que la race peut produire. La réglementation au jour le jour devrait être axée sur la biologie des saumons et non sur le bon plaisir de l'homme. Une réglementation expérimentale ne devrait être entreprise qu'avec engagements convenables envers une recherche à long terme. Sans ces mesures, on peut se demander si le but but proposé sera jamais atteint.

Received May 29, 1978
Accepted October 4, 1978

Reçu le 29 mai 1978
Accepté le 4 octobre 1978

The First Phase — Discovery

A little less than a century ago it would probably have been safe to say that research on Pacific salmon had not started, and that management based on research findings was virtually nonexistent. To be sure, there had been some famous itinerant naturalists through the northern Pacific, and the Pacific salmon had been classified (at least for the first time, if not for the last). As well, many European expatriates had come to Western North America with a baggage of plus fours, fly rods, and salmonid folklore. But there were no biological stations; no university research centers; and no programs for long-term investigation. The fisheries regulations, such as they were, were accordingly inspired almost as much by chivalry as by biology.

It was instantly evident, of course, that salmon went to sea, and from various fragments of circumstantial evidence, that they probably returned as adults to their native streams. It was also known that obstructions like dams might frustrate salmon. As early as 1902, John Pease Babcock worked mightily on building a fishway past a goldminer's dam on the Quesnel River in British Columbia. His well-documented efforts (Anon. 1961) were no doubt duplicated on a lesser scale many times over by his colleagues, and by the many salmon-minded citizens of the West Coast. It was also evident at an early date that at least some races of sockeye salmon had a 4-year life span, for the big runs came 4 years apart; that sockeye spent a year or more in the lakes, and coho a year or more in streams. This was the kind of knowledge that seeped into the pores of any outdoorsman of average intelligence.

Much of this elementary natural history was first dealt with systematically by Gilbert (1913, 1914–25) on the basis of scale readings of salmon that were being routinely taken up and down the coast in conjunction with collection of statistics on catch. Some early marking experiments seemed to confirm the notion that salmon returned to their streams of origin (Foerster 1968), though it had to be admitted that the marked fish were only looked for where they were expected.

Through the first 30 years of this century, evidence of this kind was compiled on both sides of the North Pacific. It may suffice to summarize the early descriptive research to mention the information bulletin prepared by Babcock in 1931. In a concise fashion, it outlines what remains the essence of our present understanding of the basic qualitative life history information on Pacific salmon. It does not speculate on where salmon go when they go to sea, nor does it develop any notion of population dynamics that could be used as a basis for management.

The fisheries for salmon were intense, even at the turn of the century, and some obvious features of the inshore migration were apparent (such as the catch of Fraser fish in United States' waters, which Babcock foresaw as an injustice). But, despite their intensity, the fisheries were not conspicuously regulated for ensuring particular escapements of the various races of fish to their various spawning grounds. The characteristic operational pattern of the 100-odd salmon canneries on the North American Pacific coast in 1891 was to fish flat out, knocking off only for the weekend, catching until either all the ice was gone, or all the cans were full. In consequence, the early season runs of salmon were the first to be decimated, and only subsequently were the later runs overharvested. The Alaskan fisheries were in theory constrained by the White Law of 1924, which provided that 50% of each run should be allowed to escape to spawn; but in Alaska, as elsewhere, the law was one thing and the practices of the fishery were often something else. There was no limitation on the number of salmon fishing licences, and despite an increasing pattern of restrictions on where and when fishing was allowed, regulation and enforcement were evidently not up to dealing with the complexities of harvesting the several thousand races of the five species of salmon. The early fisheries no doubt had many adverse effects that will never be documented.

Meanwhile, there were obvious impacts of other human activities on the environment of salmon — to name a few: logging changed runoff patterns and obstructed streams; mine tailings polluted streams; and irrigation projects diverted streams.

While there were some expressions of concern at these events, there was a prevailing optimism that things would be all right. Even before the turn of the century many people had begun dabbling in hatcheries (for example, Hume 1893), and when you had counted 3000 eggs in a female salmon, it didn't take more than a few minutes of calculation to have a number bigger than would fit on the back of an envelope. A vigorous program of building fish hatcheries, and an entrained program of planting fish here and there, began in British Columbia in 1884 (Larkin 1974), just about the time as similar programs from California to Alaska. Coupling enthusiasm for hatcheries with vigorous environmental protection and better regulation of the fisheries seemed to give sufficient promise for the future.

These were the perceptions that carried fisheries research and management well into the middle of the 20th century, and that persist as the major perceptions today. The standard religion was then, and is now, that adequate husbandry of the Pacific salmon as a resource requires

1. *research* on the biology of salmon;
2. *regulation* of the fisheries to ensure sustained yield;
3. *protection* of the environment to ensure the means of production; and
4. *enhancement* of natural conditions to augment natural production and to mitigate the effects of imperfect regulation and protection.

It is the thesis of this essay that these perceptions will not be sufficient for the future; that the current prospect for natural populations of salmon is a long, slow decline in abundance; and that only a major change in attitude will make it otherwise. For convenience, the focus is on Canadian contributions to the biology of Canadian salmon, which is only a part of the international literature, but which is, nevertheless, sufficient for the purpose.

The Second Phase — Gaining Understanding

After the first burst of scientific research established some of the simple life history facts of salmon biology, a second phase of research developed some appreciations of the arithmetic of salmon abundance. The first and obvious place to turn was to the early life history stages, because then the salmon were easily observed. Moreover, it was readily rationalized that the freshwater environment was more variable than the ocean, or so at least it seemed, if you couldn't afford to look much at the ocean. Led by Clemens, their Director, Foerster and Ricker (1941), Canadian researchers working largely out of the Nanaimo Biological Station, gave a strong limnological twist to their studies of sockeye salmon (*Oncorhynchus nerka*), particularly in Cultus Lake. Pritchard (1948) and his successors, notably Neave, also all working out of Nanaimo, devoted attention to the early life history of pink salmon (*O. gorbuscha*); and Wickett (1951), still another from Nanaimo, worked on coho (*O. kisutch*). By the early 1950s it was clear that though the freshwater part of the life cycle had an indispensable role to play in determining production, it was not the sole determinant of abundance. Marine conditions were also at work in varying survival from one generation to the next.

As these studies were proceeding, other investigators were trying to make sense of the mass of statistical information that had been accumulating from the routines of sampling the commercial catch, and estimating by eye the escapement to spawning grounds. The various government agencies up and down the coast conducted continuing and frequently xenophobic analyses of catch and escapement statistics, at best to achieve inspiration for management, and at least to provide some mumbo jumbo to rationalize their regulations after the event of the season's fishery.

More systematically, Milne (1955) interpreted the statistics of the Skeena fisheries as well as those of the troll fisheries along the west coast (Milne 1964), and Neave (1952) and Hoar (1951) reviewed the odd- and even-year oscillations of pink salmon populations. These studies, together with a number of studies by United States and Alaska biologists (the distinction is deliberate), and by others for salmon on the Asian side of the Pacific, built the base of confusing numbers on which speculation about salmon population dynamics was built. A major unification of these statistics was brought about by Ricker (1954), whose famous paper on "stock and recruitment" is still the cornerstone for theorizing about salmon population dynamics.

Management of salmon during this period was guided by the increasing conviction that the fishery had to be more vigorously regulated if salmon were not to be overharvested. The circumstantial evidence of success by the International Pacific Halibut Commission in restoring halibut abundance by curtailing fishing effort had its impact on salmon managers. After a protracted negotiation that began shortly after the 1913 slide at Hell's Gate in the Fraser canyon, the International Pacific Salmon Fisheries Commission was established in 1937 and began the work of rehabilitating the Fraser stocks.

The fishermen knew, too, that things weren't what they had been — that some of their number were what they called "stream robbers." Caught up in the prevailing enthusiasms for conservation, the fishermen advocated stricter enforcement and more scientific management. In some measure they got it, for the forties and fifties saw an increased attention to curtailing fishing seasons and pouncing on poachers, and an increasing effort to achieve management by stocks. The rapid apparent recovery of the up-river Fraser stocks of sockeye, attributed partially to the Hell's Gate fishways and partially to the regulation of the fishery, made it logical and popular to establish something similar in the north

— the Skeena River Management Committee. In short, management based on numerical assessments of catch and escapement of each race became firmly entrenched.

At the same time, the protection of salmon stocks became a more systematic matter. The network of fishery officers was augmented, and the first cadre of headquarters technical personnel was hired. The institutional procedures were developed to ensure that the Department of Fisheries would know early enough when salmon might be affected. All water licence applications were examined, a provincial Pollution Control Board was established (Goode and Larkin 1954), and streams were more or less regularly monitored for changing conditions.

The same happy state of incremental development was not true for the programs of fish culture. It had become apparent in the 1930s that many of the more lavish promises of fish hatcheries were not being realized, and it became increasingly fashionable to ask if they were doing anything useful. When the studies on Cultus Lake (Foerster 1938) concluded that it couldn't be proven that hatcheries were improving matters, it was decided, for the financial reasons that pervaded the late 1930s, to discontinue the federal government fish culture operations in British Columbia. The provincial government took over some of the facilities and some of the personnel for trout culture, and the rest faded bitterly away.

The Third Phase — Impacts From Outside

The third phase of salmon research and management had roots in what had gone before, but largely owed its development to events that were imposed from "outside" — the growing pressures for exploiting hydroelectric potentials of British Columbia streams, and the signing of a treaty by Japan, the United States, and Canada.

The pressures for hydroelectric development were only the spearhead of the broader pressures for what was then called "progress," but they posed a particular set of problems for biologists and engineers. The stop-log dams of former days could be bypassed with fishways of modest proportions, employing bush carpenter construction techniques. The newer dams were higher, and what proved to be just as significant, they were wider. Before the salmon attempted to climb up the fishway, they had to find the entrance. What is more, the new dams posed two alternatives for young salmon going to sea — a roller coaster ride down the spillway, or a high pressure dash through the turbines. Leaving the technical details aside (they are well covered in the book by Clay 1961, and by Andrew and Geen 1960), it is sufficient to remark that the 1950s were characterized by a major emphasis on research concerned with the engineering and biology associated with getting adult salmon up over dams, and getting young salmon back down again in fit condition to go to sea. A great deal was learned about the physiology and behavior of salmon, the work of Brett and his associates at Nanaimo (many of them being former students of Fred Fry) being most notable.

In the United States at the same time, similar developments on a more grandiose scale resulted in a variety of technological extravaganzas that clearly demonstrated that even the best of intentions couldn't save salmon populations from suffering some effects when a series of high and wide dams blocked a major river system. The whole era more or less came to an end on both sides of the border with the assessment of the problem of protecting salmon if the Columbia River was diverted and a series of dams was built in the Fraser River canyon. Even though the scheme was only a chauvinistic ploy in the negotiation of the Columbia River Treaty, nevertheless, it brought the salmon questions clearly into focus. The fish protection facilities required would cost an estimated $300 million, and there was no assurance that they would do the job. Similar conclusions were reached about the proposal for a Moran dam — a 700-foot dream on the Fraser River just above the confluence with the Thompson River. With these assessments, power corporations began to look a little harder for streams that didn't have salmon, and at other sources of electrical energy.

While this was going on "ashore" so to speak, there were major new discoveries on the high seas. The International North Pacific Treaty of 1954, among other things, set a provisional line in the North Pacific Ocean (175°W) east of which the Japanese agreed not to fish for salmon — provisional until studies could establish a line that would "equitably divide" the ocean. Though an agreement as to what "equitably divide" might mean has still to be achieved,[2] the studies that disclosed the ocean migrations of salmon were the highlight of salmon biology of the late 1950s and early 1960s. Biologists and oceanographers of the three countries contributed, each in characteristic style, to gaining new perceptions of where salmon went when they went to sea. Salmon went much further afield than most had guessed, and in varying degrees carried with them evidence, such as parasites and scale markings, of where they had come from and where they would return (see the various Bulletins of the INPFC).

The impact of these discoveries was twofold. On the management side, it became fairly clear who was catching whose salmon where and when. The interception by one country of salmon that originated in another country would not be countenanced if it could be demonstrated that the country of origin was managing so as to achieve maximum sustained yield. (This was the implication of the so-called "abstention principle" as it applied to salmon.) It accordingly became necessary

[2]In April 1978, Japan agreed not to fish east of 175°E, 10° west of the provisional line, nor within the 200-mile limit around the Aleutians, virtually assuring there would be only tiny catches of North American salmon.

for Canada and the United States to convince the Japanese that contemporary management was taking the maximum sustained yield from the various stocks that the Japanese might encounter in their high seas fishery west of the provisional line. And along the North American coast, Canada and the United States, to maintain consistency with their arguments vis-a-vis Japan, had to come more firmly to grips with their own mutual problems of interception. To curtail the catching of mixed stocks offshore, so-called "surf lines" were drawn, being literally along the surf along most of the outer coast, but 4 miles out along the Alaskan islands.[3] But there were still major problems of interception in the north, where the Alaska panhandle and British Columbia meet at 54°40′, and in the south where the international boundary meanders in its arbitrated course across the migration routes of salmon destined for Howe Sound in Canada, south to Puget Sound in the United States.

These were difficult problems, and the grappling has now gone on for over 20 years without agreement. Nevertheless, the arguments have been productive, for they have had perforce to deal in a rigorous way with all the details of regulating the salmon fisheries. Inadequate regulation was a conspicuous embarrassment that had to be overcome. Salmon fisheries became an international example of speedy and sophisticated assessment of how many of which run were being caught, and of how many were escaping. The stage was set for the evolution of a well-researched management dinosaur, distinguished by its elaborate machineries for day-to-day regulation.

Of equally profound significance, the revelations of the complex marine migrations of salmon posed two questions: "What influences marine survival?" and "How do salmon navigate so as to find their way home?" Parker (1966), with his studies in North Bentnick Arm (Burke Channel), and Ricker (1964), with his assemblies of high seas statistics, established that the mortalities of *young* salmon at sea were probably more variable and more intense than those of the more mature fish. But studies of mortality and growth at sea are notoriously expensive, and much less was done than would have been desired.

Nevertheless, there were some important speculations about salmon population biology. The demonstration that salmon were vulnerable to greater proportionate mortality when they were less abundant (the depensatory mortality of Neave 1952) opened the way to further explanation by Ward and Larkin (1964), and Larkin (1971) for cyclic dominance of some races of sockeye salmon (Ricker 1950). It also helped explain why populations of pink salmon, when once depressed, might wait a long time to recover. Additionally, for the first time, there was sufficient knowledge of the seaward migrations and ocean life history of salmon to begin to conceptualize how the various populations of the various races were sharing the grazing resources of the North Pacific.

There were also advances on the question of how salmon navigate, for the qualitative facts of distribution and the recoveries of marked fish could only comply with certain interpretations. Salmon clearly had the equivalent of a clock, a map, and a compass. Spurred by the discoveries that birds and bees could use celestial clues for direction finding, it was sensible to ask if fish could do the same. Led by Hasler's work (1960) on perch, Groot (1965) demonstrated in his superb studies on Babine Lake that young salmon certainly could use signs in the sky to guide their seaward migration. At about the same time, Hasler (1966) was also demonstrating that salmon could use olfactory clues as well to find their way home, once they had found freshwater or were in its range of influence. For a brief period, these findings seemed to have sketched out the broad explanation of homing; but in a review that has become a classic, Royce et al. (1968), assembling all the marine evidence, identified the need for much more research to account for the remarkable things that salmon did in their wanderings at sea, specifically identifying the potential use of sensory perception of electromagnetic fields. Without question, the period from 1950 to 1965 was marked by major advances in understanding the biology of Pacific salmon. Except for a nagging concern about an almost comprehensive ignorance of salmon genetics, researchers were in general satisfied that qualitatively at least, and in some measure quantitatively, salmon biology was reasonably in hand.

There is an important postscript to this brief sketch of the third phase of salmon research and management — economics became an overt consideration. The fishery for salmon was a conspicuously intense activity involving many people and a fair share of politics. The *routines* of regulation included daily radio–telephone consultations on details of catch by area and even, where necessary, 24-hour service on scale reading analysis of the racial composition of the catch. Fishing started promptly at 6 PM. Sunday evening and continued under continuous surveillance until a closure some day later in the week. The blitzkrieg intensity of the fishery, coupled with demands by the various kinds of fishermen (seiners, gill netters, trollers) for a fair share of the catch, together with the declared intention of management to achieve optimum escapement of each stock, required great skill in regulation, cool nerves in the crises, and a good measure of blarney in subsequently rationalizing decisions. It was little wonder that economists were attracted like wasps to a picnic lunch.

Predictably, the economists were quick to question whether this was efficient and were immediately misunderstood by the industry and by the biologists who saw it all as much too efficient. What the economists meant, of course, was that it was costing too much to

[3]This anomaly came about from some alleged misunderstandings in the late stages of negotiation and subsequently led to some biliousness on the part of the Canadians.

take the harvest and that the whole operation wasn't contributing as it might to National Revenue. (The capitals are intentional because the economists say it that way.) The same sort of thing was characteristic of many other fisheries in the world. Canadian economists were thus prompted to make contributions to an international discussion that eventually culminated in Garrett Hardin's (1968) generic conception of the tragedy of the commons.

On a less philosophical level, it had come time to consider what was seen by economists as a necessity — limiting the fishing effort on salmon. It was appreciated that 85% of the permissible Pacific salmon catch could be taken with about a dozen strategically placed traps,[4] and the remainder could be cleaned up by a small mobile fleet that could also be used for retaliatory demonstrations if the United States go out of line by intercepting Canadian fish. The stage was set for a new and frustrating stanza in the annals of salmon management and research.

The Fourth Phase — Inspiration

By the late 1960s it had become apparent that the management of salmon was concerned with a complex economic-socio-politico-ecological system, to use the jargon of that time, which had to be glimpsed in all its horrendous holism if the future were to unfold as it could. This realization, combined with the advent of computer capacities, brought about the salmonid version of the Age of Aquarius. At first, the computers were addressed to the simple matter of confirming that Ricker was indeed correct in his surmises (which surprised Ricker least of all), and in exploring various themes in the population dynamics of salmon for which speedy arithmetic was a perfect answer to analytical recalcitrance (see Larkin and Ricker 1964; Tautz et al. 1969, for examples of this transitional stage). But it wasn't long before much more comprehensive issues were being examined using much more elegant programming architectures for examining systems behavior. With Paulik and Greenough (1966), and then Walters (1969) in the vanguard, the expertise was developed for almost instant perceptions of the consequences of any chosen course of action, given, of course, a large number of assumptions that only might be true and/or sensible.

The revelations of computer-projected scenarios were treated with considerable skepticism by those who had responsibilities for management, and usually for the wrong reasons (such as because they didn't do them), even though there were good reasons (such as they were done too hastily). Fortunately, the events of the day were more than sufficient to sensitize managers to the demands for ever more intensive management. The fishery became characterized by 2 days or less fishing per week, which by simple logic suggested that the fleet had at least 2½ times the capacity necessary for a 5-day week. The economists, it seemed, were right — it was time for action. License limitation, the ostensible way to control the fishery and to restore its economic health, was launched with appropriate unction — and from an economist's viewpoint, almost immediately developed into a fiasco. Only the least effective fishermen were purged, and those who stayed in decided to upgrade their equipment. Fishing effort was not decreased but instead became more mobile and effective than it had ever been.

Meanwhile, the international problems with the United States dragged on, exacerbated by the catch of U.S. hatchery-reared coho and chinook salmon by Canadian fishermen, especially on the outer west coast. Sportfishing, despite all its hilarities, began to show considerable signs of being a factor rather than a triviality in salmon abundance. Research on salmon population dynamics became typically to be more of the same, concerned largely with how to fine-tune an evidently cumbersome and antiquated system.

At the same time, the continuing economic development of British Columbia brought increasingly greater pressures on the *environment* of salmon. Almost everybody, and especially the man on the street, perceived a decreasing prospect for protecting salmon from the multitude of encroachments on their habitat. Researchers responded to the social concerns about environmental issues by focusing on the effects of a wide spectrum of pollutants on salmon, and by attempting to pinpoint the ways in which other resource uses, such as logging, might affect salmon. Estuaries, which had been formerly treated as a no-man's land between the rivers and the sea, began receiving the attention they deserved. But the most common complaint of fisheries personnel became that they couldn't be everywhere at once. Increases in staff only led to the uncovering of more reasons for concern. There was an increasing realization that salmon populations were destined for a steady abrasion by the fishery on one side and environmental degradation on the other.

In these circumstances, an inspiration was clearly necessary, and it took the obvious route of a resurrection of erstwhile hopes for using fish cultural techniques. In one blow, two problems could be solved — how to find enough fish to occupy the fleet, and how to compensate for the loss of salmon habitat. Enter "SALMON ENHANCEMENT," ushered in with some sweeping generalizations and reassurances, such as those of "Play it Again Sam" (Larkin 1974), which captured the mood of the late 1960s and early 1970s.

Like most inspirations, the Salmonid Enhancement Program (SEP) was really not that new an idea. As early as the late 1950s the engineers and biologists of the then-called Resource Development Branch of the then-called Federal Department of Fisheries, had been

[4]Curiously, traps were banned in Alaska as unfair, and the last trap in British Columbia, at Sooke, was phased out in the 1950s.

led to consider fish hatcheries and their like as mitigating devices where fishways and their like wouldn't work. The International Pacific Salmon Fisheries Commission took similar steps on the Fraser River and bogged down only because Canada decided not to get involved in sharing costs with the United States for fear of enhancing U.S. arguments for a share of the catch. As well, developments on a larger scale were taking place in the United States where hatcheries had never gone as far out of style as they had in Canada. But for one bureaucratic reason or another (which, translated, means Treasury Board), the Canadian department had been slow to implement *major* programs of enhancement activities. By the early 1970s, the time was ripe for initiatives.

Confidence in fish culture techniques had been steadily growing since the 1950s. Following the well-beaten track of the farm animal scientists, a substantial literature had been developing on fish nutrition. An arsenal of sulfa drugs and antibiotics could be brought to bear on fish diseases by an increasingly better informed group of "fish doctors." There were many new wrinkles in the design of facilities for rearing and transporting fish. Hatchery practices had at long last graduated from wizardry to science. Moreover, there had been a growing experience of success with techniques that were less obtrusive into the natural habits of salmon, such as spawning channels and flow regulation schemes. Finally, there was a much broader base of understanding of the natural limits to production, and a greater variety of techniques for adequate evaluation of whatever was attempted. Some notes of warning were sounded about disease transmission and genetic effects and, true to style, economists were hesitant without firm cost/benefit estimates. The Salmonid Enhancement Program was accordingly launched in a mood of optimism regarding success tempered by concern for ensuring and demonstrating that the evaluation of the program would be ecologically responsible and economically rewarding.

Once planning was seriously under way, it became apparent that enthusiasms for a quick doubling of the numbers of salmon had to be quenched by the appreciation that hyperefficient hatchery practices would have major potentials for creating many kinds of mischief. In addition to the biological questions concerning the impact of cultured fish on the genetics and disease risks of wild fish, there were the more immediately troublesome questions centered on how to harvest the fruits of enhancement without damaging natural production. Enhancement could only be undertaken on a large scale if it was fully and carefully integrated into a total system of management.

These are the kinds of issues that require a great deal of careful analysis and that can be usefully explored with computer simulations. In due course, appropriate workshops were organized, with the usual initial rites of expression of false modesty on the part of the computer experts (chiefly Carl Walters), and of skepticism flavored with open-mindedness on behalf of their planners (the SEP personnel). It was almost immediately confirmed (I am told) that there was much more to the strategic planning of enhancement than many had realized. Such data as there were needed assembling. There were large gaps in the data, especially concerning the behavior of the fishing fleet. Given reasonable assumptions about what was not known, the simulations clearly projected the potential need for much more sophisticated management of what was already the most sophisticated fishery in the world. From a purely technical point of view concerned only with the mechanics of the fishery interacting with the dynamics of salmon populations, enhancement that was single-mindedly concerned with production could drive management as it had never been driven before.

To make matters worse, as the program planners were daily reminded, the total system had many social dimensions. Which of the various kinds of fishermen were to gain from the enhancement? What emphasis was to be given to different regions of the coast? Were the various users to be taxed in proportion to what they caught, in proportion to the enhancement production that they caught, or were they not to be taxed directly at all? Was the program to be handled by the federal government, by the federal and provincial governments in concert, or otherwise, such as by a Crown corporation? Was the Fraser River to continue to be out of bounds for enhancement until there was agreement with the United States on interceptions? Would successes in enhancement lead to the abandonment of protection? Increasingly, the inspiration of enhancement was blunted by the realization, so common nowadays, that you can't fiddle with one part of a system without creating reverberations in the rest of its parts. Big dinosaurs most readily evolve into even bigger dinosaurs.

But, as all good planners know, awareness of problems is half of their solution. The Salmonid Enhancement Program was accordingly launched in a highly participatory mode, with a downpour of committee meetings and consultations, a wide variety of program proposals, and exhaustive justification to Treasury Board. The resulting activities (McDonald 1977) are indeed an inspiration that is best characterized by its broadness and balance, and an appropriate modicum of research and evaluation. If the program is continued as it has been conceived, it holds promise of using a wide range of techniques for increasing the abundance of *all* species of salmon and steelhead in *all* regions of the coast to the benefit of *all* sectors of the fishery, and at the same time to substantially further the technologies of enhancement.

A Prognosis for the Fifth Phase — Getting There From Here

From time to time, salmon managers are obliged to

state their "objectives" so that they may demonstrate to their superiors that their operations are guided by an appropriate hierarchy of thought processes. Fundamental to all of these exercises, as far as salmon fisheries are concerned, is the recognition that the resource must be kept healthy, which means maintaining a full spectrum of genetic variability in the widest possible range of environments (Loftus 1976). In essence, it means looking at things from the viewpoint of the salmon.

To salmon, national boundaries are meaningless, the price of fish is irrelevant, and there are no consolations in satisfying arbitrary recipes for optimal social conditions among fishermen, nor in participating as one of the actors in multiple resource use. Protection, regulation, and enhancement should thus be bent to serve the interests of salmon as a resource rather than to those who use the resource. From such a perspective, several recommendations for present management of the fishery are more or less inevitable. In addition to the continuing needs for protection and enhancement, there are the following concerning regulation.

First, the next generation of any stock of salmon should not be the object of an economic gamble. It has become fashionable to speak in the jargon of discounting as though the objective of management was to maximize the long-term economic rent from the salmon harvest. It may thus seem to make short-term sense to let the fishermen overharvest this year so they won't have to go on some form of social assistance, justifying the risk to salmon populations by seeing it as a trade-off in a larger economic system. This is a perverted philosophy that places the responsibility for the future on the shoulders of the salmon. Under *no* circumstances should the permissible harvest of any race of salmon be knowingly exceeded. No minority group, no economic stress, no social pressure should prevail over the common sense of providing as best we can for the future. Certainly a salmon would say, "Don't discount me."

Second, flowing from the foregoing, the day-to-day regulation of the fishery must be geared to what is meaningful in salmon biology, not to what is convenient to fishermen or the fishing industry. For example, the traditional 6 PM Sunday opening is pure Alice in Wonderland. At a turn of the tide that is a matter of chance, it launches a large fishing effort that is sustained until it is judged that a certain number of fish will *subsequently* escape the fishery and get past an upstream boundary by 6 PM the next Sunday. Far better would be systems allowing more precision, such as fishing every 3rd day and adding extra days if it seemed appropriate; or permitting a part of the fleet to fish on some days and another part on other days, and timing the openings to stages of the tide. There are also the possibilities of limiting licenses to fishing only in certain areas at certain times, thus controlling the concentrations of fishing effort on concentrations of fish. In brief, regulation of the fishery must be built around the absolute necessity of obtaining escapements that are adequate both qualitatively and quantitatively, rather than around any of the social and economic circumstances of the fishery. Salmon, the resource, come first.

Third, and finally concerning regulation, the time has come for experimental management in the best sense of the word "experiment." Much of what is alleged to be effective regulation may well be much less effective than other ways of proceeding. Curiously, while the practices of the present fishery have been extensively documented, there has been virtually no attempt to try other ways in carefully monitored studies. The fishery has been taken as a "given," something to be coped with in regulation, rather than as a potential variable to be manipulated. While it is comforting to do things as they have been done, it is not productive of new knowledge.

Experimental assessments of management effectiveness are of necessity long-term undertakings, and it is one of the realities of management research that the length of time a biologist is in charge of a project is often much less than is necessary to adequately test ideas. It is also a reality that for those not familiar with biological research, 10 or 20 years seems an inordinately long time to investigate any problem, even though it is a matter of simple arithmetic to point out that two generations of sockeye salmon at 5 years apiece consume 10 years. It is the sad truth that in the past two decades, along the Pacific coast, literally dozens of long-term management research projects have evolved from great promise into nothingness with only a short intermediate stage of scientific productivity. From these experiences it is essential to assert the necessity for long-term research and the administrative devices to ensure it. To do otherwise, from a salmon's point of view, is a sure way to continue to make the same mistakes in management.

The present circumstances of the salmon fisheries contain many elements that make bumptious optimism an inappropriate state of mind. The pressures of other resource uses continue to threaten salmon environments. The techniques of enhancement are still imperfect, and only a sustained program involving adequate research and evaluation can ensure success. Of greatest concern, the fisheries, both sport and commercial, are increasingly capable of overharvesting stocks. Even if the present system of regulation were executed with flawless technique (which it isn't), it is not *demonstrably* satisfactory as a way of harvesting each race of salmon appropriately. Add in the compromises for ostensibly good social, economic, and political reasons, and the salmon are indeed faced with tough prospects.

The only realistic prognosis for salmon is a long and slow decline in abundance, tempered only by the amelioration of some of the effects of environmental attrition and the fisheries by an array of enhancement

techniques. To make it otherwise will require outspoken recognition of the present situation and a commitment to experimental management coupled with long-term research. To achieve a doubling of present levels of abundance with our current attitudes doesn't look all that likely: Maybe we can't get there from here.

ANDREW, F. J., AND G. H. GEEN. 1960. Sockeye and pink salmon production in relation to proposed dams in the Fraser River system. Int. Pac. Salmon Fish. Comm. Bull. 11.

ANON. 1961. The Quesnel story. Int. Pac. Salmon Fish. Comm., New Westminster, B.C.

BABCOCK, J. P. 1931. The Pacific salmon. B.C. Fish. Dep. Bull., Victoria, B.C.

CLAY, C. H. 1961. Design of fishways and other fish facilities. Can. Dep. Fish., Ottawa. 301 p.

FOERSTER, R. E. 1938. An investigation of the relative efficiencies of natural and artificial propagation of sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. J. Fish. Res. Board Can. 4: 151–161.

1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. 162: 422 p.

FOERSTER, R. E., AND W. E. RICKER. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. J. Fish. Res. Board Can. 5: 315–336.

GILBERT, C. H. 1913. Age at maturity of the Pacific coast salmon of the genus *Oncorhynchus*. Annu. Rep. B.C. Fish. Dep. 1912: 57–70.

1914–1925. Contributions to the life-history of the sockeye salmon. Papers 1–10. Annu. Rep. B.C. Fish. Dep. 1913–1924.

GOODE, N. J., AND P. A. LARKIN. 1954. Pollution . . . and You. Trans. 7th B.C. Natural Resources Conference 7 p.

GROOT, C. 1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of lakes. E. J. Brill, Leiden. 198 p.

HARDIN, G. 1968. The tragedy of the commons. Science 162: 1243–1248.

HASLER, A. D. 1960. Guide posts of migrating fishes. Science 132: 785–792.

1966. Underwater guideposts: homing of salmon. Univ. Wisconsin Press, Madison, Wisc. xii + 155 p.

HOAR, W. S. 1951. The chum and pink salmon fisheries of British Columbia, 1917–1947. Bull. Fish. Res. Board Can. 90: 46 p.

HUME, R. D. 1893. Salmon of the Pacific coast. Private printing. 52 p. + lithographs.

LARKIN, P. A. 1971. Simulation studies of the Adams River sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 28: 1493–1502.

LARKIN, P. A., WITH APPENDICES BY B. A. CAMPBELL, AND C. H. CLAY. 1974. Play it again Sam — an essay on salmon enhancement. J. Fish. Res. Board Can. 31: 1433–1459.

LARKIN, P. A., AND W. E. RICKER. 1964. Further information on sustained yields from fluctuating environments. J. Fish. Res. Board Can. 21: 1–7.

LOFTUS, K. H. 1976. Science for Canada's fisheries rehabilitation needs. J. Fish. Res. Board Can. 33: 1822–1857.

MCDONALD, J. E. [ed.]. 1977. Salmonid Enhancement Program Annual Report 1977. Fish. Environ. Can. Enhancement Serv. Branch, Vancouver, B.C. 84 p.

MILNE, D. J. 1955. The Skeena River salmon fishery, with special reference to sockeye salmon. J. Fish. Res. Board Can. 12: 451–485.

1964. The chinook and coho salmon fisheries of British Columbia. Bull. Fish. Res. Board Can. 142: 46 p.

NEAVE, F. 1952. "Even-year" and "odd-year" pink salmon populations. Trans. R. Soc. Can. (V), Ser. 3, 46: 55–70.

PARKER, R. R. 1966. Marine mortality schedules of pink salmon of the Bella Coola river, central British Columbia. J. Fish. Res. Board Can. 25: 757–794.

PAULIK, G. J., AND J. W. GREENOUGH. 1966. Management analysis for a salmon resource system. *In* K. E. F. Watt [ed.] Systems analysis in ecology. Academic Press, New York, N.Y.

PRITCHARD, A. L. 1948. Efficiency of natural propagation of the pink salmon *Oncorhynchus gorbuscha* in McClinton Creek, Masset Inlet, B.C. J. Fish. Res. Board Can. 7: 224–236.

RICKER, W. E. 1950. Cyclic dominance among the Fraser River sockeye. Ecology 31: 6–26.

1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

1964. Ocean growth and mortality of pink and chum salmon. J. Fish. Res. Board Can. 21: 905–931.

ROYCE, W. F., L. S. SMITH, AND A. C. HARTT. 1968. Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. U.S. Fish. Bull. 66: 441–462.

TAUTZ, A., P. A. LARKIN, AND W. E. RICKER. 1969. Some effects of simulated long term environmental fluctuations on maximum sustained yield. J. Fish. Res. Board Can. 26: 2715–2726.

WALTERS, C. J. 1969. A generalized computer simulation model for fish population studies. Trans. Am. Fish. Soc. 98: 505–512.

WARD, F. J., AND P. A. LARKIN. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pacific Salmon Fish. Comm. Progr. Rep. 11: 116 p.

WICKETT, W. P. 1951. The coho salmon population of Nile Creek. Fish. Res. Board Can. Progr. Rep., Pacific Coast Station. 89: 88–89.

BOOK REVIEWS/COMPTES RENDUS

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Marine Pollutant Transfer. *Edited by H. L. Windom and R. A. Duce. D. C. Heath & Co., (Lexington Books), Lexington, Mass. & Toronto. 1976. vii + 391 p. $20.95.*

This text is a summary of major findings resulting from the Pollutant Transport Program which was sponsored by the National Science Foundation, Office for the International Decade of Ocean Exploration (NSF/IDOE). A NSF sponsored workshop on marine pollutants at the Skidaway Institute of Oceanography, Savannah, Georgia in January 1976 provided a focus for discussion of the present state of knowledge and future research requirements with regard to marine pollutant transfer and these deliberations and reports formed the basis of this text. The 15 chapters are divided into major sections dealing with heavy metal and organic contaminants prefaced by a concise introduction to the major processes involved in pollutant transfer in the marine environment.

Oceanic waters interface with five major compartments, namely rivers, atmosphere, biosphere, suspended particulates, and sediments collectively forming the marine ecosystem. In the introductory chapter each interface is briefly defined and the major physical–chemical factors participating in the exchange process presented and current research and future paths of endeavor assessed. From the discussion it would appear that answers to the specific scientific questions may be readily achieved through a concerted multidisciplinary effort.

This impression is not reinforced in the following chapters which summarize the results of specific research programs. It is here that the magnitude of the problems inherent in investigations of this kind are realized. The water volume of the oceans total approximately 1.35 billion cubic kilometres with a surface area of 362 million square kilometres. The incredible dilution power exercised by this volume may be exemplified by consideration of the anthropogenic input of lead. Of the annual global production of refined lead approximately 10% or 3×10^5 tonnes enter the oceans. Studies of the flux rates of lead in the biosphere indicate that natural reservoirs of lead have been overwhelmed resulting in a 20-fold increase in the mean lead concentration in the biosphere. After decades of lead contamination, however, the mean oceanic concentration of this heavy metal is only 10^{-12} g/L and this amount is subdivided into several chemical states. Under conditions such as these, sample concentration is a constant problem and specialized procedures are required to raise the concentration of some contaminants above the limits of analytical detection. Added to these technical difficulties are questions of the relative input of the contaminants from anthropogenic sources versus natural sources such as erosion and volcanic activity.

In view of these inherent problems the six chapters on heavy metals present a credible set of models relating contaminant transfer among the various oceanic compartments. By necessity much of the work has been confined to coastal areas although the need for additional work on the open oceans is clearly identified. Greater emphasis is placed on metals arising from industrial and urban activities such as lead, cadmium and mercury although many of the arguments apply to generalized questions of heavy metal transport.

An estimated 10^6 to 10^7 tonnes of petroleum enter the marine ecosystem annually with major anthropogenic sources such as offshore oil and gas exploration and production, shipping activity and land-based industrial activities accounting for the great majority of this input. Surprisingly little is known about the fluxes of petroleum-derived contaminants within the marine ecosystem although several recent studies are discussed in four chapters of this text. The complex and variable mixture of hydrocarbon constituents can be roughly segregated in low molecular weight residues of N ranging from 6 to 20 and the so called "particulate tar" components (N of 21–40). Clearly the physical and chemical properties such as water solubility, volatility and stability of each class of compounds have a major effect on their exchange processes across the six interfaces identified in the marine environment. Pelagic petroleum appears to change radically in chemical composition through the action of many processes including evaporation, solubilization, photo-oxidation, physical disintegration as well as biological activity although these processes may act sequentially rather than simultaneously. The presence of high concentrations of biogenic hydrocarbons complicates the identification of petroleum-derived organic especially with respect to decomposition products. Although petroleum pollution is increasingly evident in the marine environment it is clear that a major scientific effort will be required to provide an adequate model of the transfer of these contaminants.

The final four chapters deal with synthetic halogenated hydrocarbons, predominantly PCBs, DDT, and their derivatives. An impressive overview of the distribution of these materials in the atmosphere, oceans, polar ice caps and biota from diverse areas of the globe is presented although the data are scattered in numerous tables. Atmospheric transport appears to be a prime vehicle for global dispersal of these contaminants although 5000 tonnes of PCBs were introduced directly into North American rivers and coastal waters in 1970. At the ocean biosphere interface the massive dilution power of the oceans is partially offset by bioaccumulation factors as high as 10^5 to 10^6 in certain marine biota. Tissue levels of specific halocarbons sufficient to produce toxic effects have been recorded in marine biota, especially birds, for a variety of geographic areas. Although some data are available for a few specific halogenated hydrocarbons, sufficient information on the interface flux rates and rates of removal from the biologically active regions of the marine ecosystem does not exist to assess the long-term impact of these contaminants. Fortunately recent controls on the manufacture and use of some of the more toxic and persistent materials have resulted in a major decrease in their rate of input to the oceans.

This volume is of some value as a source of reference information on marine contaminants and as a summary of recent thinking on mechanisms of pollutant transfer in the marine environment. Perhaps of equal value, however, is the appreciation of the enormous complexity the studies required to achieve an understanding of the interactions among the numerous compartments of the marine environment and anthropogenic inputs of a wide variety of contaminants.

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(R179)

Disease Diagnosis and Control in North American Marine Aquaculture. Developments in Aquaculture and Fisheries Science, 6. *Edited by Carl J. Sindermann. Elsevier Scientific Publishing Co., New York and Amsterdam. 1977. xii + 320 p. $39.95.*

This book is a valuable and comprehensive addition to the field of diagnosis and control of marine aquatic animal diseases, major obstacles to success in intensive culture. Although it is written primarily to aid marine culturists experiencing disease problems in North America, the coverage is broader than the title implies. It includes, for example, descriptions of diseases of freshwater shrimps, certain diseases that occur outside North America, and the disease distribution reported on a worldwide basis.

The first two short chapters introduce the general subject of disease, stressing the need to avoid an overly simplistic approach. The critical requirement for correct diagnosis is coupled with the reminder that disease problems are often the products of poor husbandry and not just the result of invasions by specific pathogens.

The major portion of the book is written in a highly standardized handbook format in which separate chapters are devoted to Crustacean Diseases, Molluscan Diseases, Fish Diseases, and Marine Turtle Diseases; each chapter is then divided into major sections relating to the different animals in the class. A short chapter introduction is followed uniformly by a concise synopsis of the section material to be covered. In the individual sections, e.g. Shrimp Diseases, each disease is treated separately in a concise fashion under the headings of Common Name, Species Affected, Gross Signs, Cause, Method of Diagnosis, Life History (Biology and Epizootiology), Effect on Host, Preventive Measures, Known Geographic Distribution, and a list of Key References. Wherever possible, relevant and good photographs are included to illustrate the salient features of the disease under discussion. Approximately 70 separate diseases, covering the species most frequently cultured in North America, are accorded this treatment; most are understood sufficiently to permit detailed characterizations. A few others for which definite etiologies are lacking are described as syndromes under general names, e.g. Cramped Tails of Shrimps. All of the disease descriptions have been written by scientists actively engaged in studying the particular disease or are practitioners in the area of interest. Thus, the work is reliable and authoritative and gives the culturist straight-forward and practical measures to reduce the impact of or eliminate the problem.

The book is completed by several brief but sound, highly pertinent chapters on Environmental Contaminants, Dietary Deficiency Diseases, Vaccines and Disease Resistance, Disease Problems Created by Introduced Species and three appendices of General References, Disease Research Groups, and a list of Chemotherapeutic Agents. The chapters reflect the editor's broad interest and knowledge and his commonsense approach in treating disease as a complex situation integrating the host, the disease agent, the environment, and husbandry.

The book has been very well planned, a fact that accounts for much of the success in making it both practical and useful to the culturist and the diagnostician. The many citations also make it a very handy reference and guide to the literature in the general disease field. As the editor points out, a major problem in producing a book such as this is to reduce the vast and unwieldy literature to manageable proportions, a feat that has been accomplished with considerable skill.

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(R196)

Introductory Dynamic Oceanography. *Stephen Pond and George L. Pickard. Pergamon Press, Oxford, England. 1978. 241 p. $16.50 flexicover, $33.00 hardcover.*

To one whose copy of Pickard's Descriptive Physical Oceanography is almost always out on loan to an interested lay person, student, or new employee, the companion volume on Dynamic Oceanography has been long awaited. In this volume, the authors have aimed to provide a readership who are not mathematicians or physicists, an introduction to dynamic oceanography presenting, deriving, and explaining the various mathematical equations with diagrams, finite difference arguments, and physical descriptions.

Topics covered include all those of classical dynamic oceanography plus a few extra. Beginning first with a chapter dealing with the physical properties of seawater, the authors move on to chapters concerning the forces acting on and in the water column, conservation of mass and volume, stability and mixing, equations of motion, nonlinear effects, and the concept of making approximations to equations using scaling arguments, geostrophic currents, wind-driven circulation models, thermohaline circulation models, numerical models, waves, and tides. The material in the chapters on wind-driven circulation, thermohaline circulation, and numerical models are presented from an historical perspective showing how the ideas developed, explaining from a physical point of view what was considered in each model, what was not considered, and most importantly how, because of the approximations made, the model's predictions might be expected to be different from the real ocean. A particular strength of this text is its delineation of the range of application of many dynamical models and techniques, thus giving to a beginning student in the field a view of the frontiers of the field and a discussion of the difficulties involved in moving beyond those frontiers.

In addition to these chapters, the authors have provided a stimulating introduction which outlines some of the many

questions dynamic oceanographers seek to answer, a brief summary of a few areas of active and current research, a simple mathematical review introducing concepts of vectors, scalars, fields, derivatives, and integrals as well as some basic fluid dynamics, a summary of units used in physical oceanography, and a bibliography giving a capsule comment on most of the available texts in physical oceanography plus some in related fields.

An introductory textbook such as this must make many choices as to what to include and what not to include. The models and concepts discussed tend mostly to be steady and linear. A reader of this book may be left with the feeling that the ocean itself is steady, linear, and regular, whereas modern measurements have demonstrated that mean currents in the ocean are much smaller than the time-dependent currents and that horizontal correlation scales of such currents are very short indeed. This concept is stated in passing within the text but a few such lines within 200 pages of description of models, etc. assuming the contrary can easily be overlooked. Also, in the discussions of waves and tides, inertial waves or internal tides are not dealt with. This is an unfortunate omission since in most current meter records these account for much of the high frequency variability and a nonphysicist who might be concerned with the effects of the physical environment should be made aware of their presence.

The authors have chosen to use scientific units throughout as well as a right-handed coordinate system. Both these are beginning to come into more use in the current literature and the reader is told about the older units and alternate conventions that are also used. There is never a best time for changing units or conventions. Use of the new sets in a first course will tend to make the older literature somewhat more difficult for the newcomer to the field but may speed the acceptance of these units in the future. To reduce the cost of the book, it has been reproduced directly from the typescript. In a few pages this certainly detracts from its readability, particularly on pages in which tables or numerous small mathematical expressions are inserted in the text. I think in future printings the typesetting of such tables might well be considered. On the whole, the text is a valuable addition to the oceanographic literature. I am sure that my copy will be absent from my bookshelf as often as is *Descriptive Physical Oceanography*.

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(R233)

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Fluctuations of chlorophyll and related physical parameters in British Columbia coastal waters **R. C. Wiegand and S. Pond**

Distribution of nutrients in the Gulf of St. Lawrence **A. R. Coote and P. A. Yeats**

Estimated escapement of Atlantic salmon (*Salmo salar*) for maximum smolt production in rivers of different productivity **P. E. K. Symons**

Estimating chlorophyll extraction biases **R. E. Stauffer, G. F. Lee, and D. E. Armstrong**

Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths **R. J. Beamish**

Tissue sources and diagnostic value of circulating enzymes in cetaceans **J. R. Geraci and D. J. St. Aubin**

Lethal and sublethal effects of binary mixtures of cyanide and hexavalent chromium, zinc, or ammonia to the fathead minnow (*Pimephales promelas*) and rainbow trout (*Salmo gairdneri*) **S. J. Broderius and L. L. Smith**

Summer plankton distributions associated with the physical and nutrient properties of the northwestern Gulf of St. Lawrence **J. M. Sevigny, M. Sinclair, M. I. El-Sabh, S. Poulet, and A. Coote**

Twilight activities of yellow perch, *Perca flavescens* **G. S. Helfman**

ATP as a measure of living phytoplankton carbon in estuaries **M. Sinclair, E. Keighan, and J. Jones**

The intrusion of fine sediments into a stable gravel bed **R. L. Beschta and W. L. Jackson**

Spectral and biochemical characteristics of the particulate matter in Bedford Basin **P. Mayzaud and S. Taguchi**

Notes

Control of rancidity in frozen Pacific herring, *Clupea harengus pallasi*: use of sodium erythorbate **E. Bilinski, R. E. E. Jonas, and Y. C. Lau**

Immersion variation of sockeye salmon (*Oncorhynchus nerka*) with two pathogenic strains of *Vibrio anguillarum* **R. W. Gould, R. Antipa, and D. F. Amend**

Expressing the phosphorus loading concept in probabilistic terms **S. C. Chapra and K. H. Reckhow**

ANNOUNCEMENTS / AVIS

1979 Annual Meeting American Fisheries Society

Call for Papers

The 1979 Annual Meeting (109th) of the American Fisheries Society will be held at West Yellowstone, Montana, on September 12–15, 1979. As in most previous years, this meeting will be held in cooperation with, and overlapping, the annual meeting of the International Association of Fish and Wildlife Agencies. Technical paper sessions will be emphasized, but proposals for symposia, modules, debates, and poster sessions to be convened by individuals or groups will be accepted until January 15.

The deadline for submission of formal abstracts to be considered for contributed paper sessions is *March 15*. Abstracts should be double-spaced on plain paper and limited to a maximum of 250 words. They should include the reason for doing the study, the objectives, and the principal results and conclusions. Each abstract should carry a title and the full name and address of each author. Indicate whether any author is a student, and what visual aids will be needed (2×2 slides preferred). Authors will be notified of the status of their submission by late May.

All proposals, abstracts, and queries should be sent to

Dr Dean E. Arnold
AFS Program Chairman 1979
328 Mueller Laboratory
University Park, Pa. 16802, USA

American Fisheries Society Réunion annuelle de 1979

Appel de contributions

La réunion annuelle de 1979 (la 109e) de l'American Fisheries Society se tiendra à West Yellowstone, Montana, du 12 au 15 septembre 1979. Comme par le passé, cette réunion se tiendra en coopération avec et chevauchera celle de l'International Association of Fish and Wildlife Agencies. On mettra l'accent sur des séances au cours desquelles seront présentés des travaux techniques, mais on acceptera jusqu'au 15 janvier des suggestions sur des colloques, modules, débats, panneaux-réclames et autres séances convoquées par des individus ou des groupes.

Les résumés dans les formes à être considérés pour les séances consacrés aux contributions devront être soumis avant le *15 mars*. Ces résumés devront être tapés à double espace sur papier ordinaire et limités à un maximum de 250 mots. Ils devront inclure la raison de l'étude, les objectifs et les principaux résultats et conclusions. Chaque résumé devra avoir un titre et contenir le nom au complet et l'adresse de chaque auteur. Indiquez si l'auteur est un étudiant et mentionnez le genre d'aide visuelle requis (diapositives 2×2 préférées). Les auteurs seront avisés vers fin mai de l'état de leur soumission.

Les suggestions, résumés et demandes de renseignements devront être adressés à

Dr. Dean A. Arnold
AFS Program Chairman 1979
328 Mueller Laboratory
University Park, Pa. 16802

Environmental Physiology of Fishes
Summer Course

An Advance Study Institute (ASI) on the Environmental Physiology of Fishes will be held under the auspices of the NATO-Scientific Affairs Division, Université de Montréal and Bishop's University from August 12 to 25, 1979 in Lennoxville, Québec, Canada. About 16 leading workers in the field will deliver lectures on the role of chemical and physical factors on the physiology of fishes as well as the responses of fishes to a combination of these factors (rhythms, behavior etc.). About 80 participants at the postdoctoral or senior postgraduate level will be chosen to attend from among the applicants. Preference will be given to citizens of the NATO member countries, some of whom may also be awarded financial assistance towards travel and/or living costs.

Interested persons may contact the director of the ASI:

La physiologie environnementale chez les poissons
Un cours d'été

Un cours d'été sur la physiologie environnementale chez les poissons aura lieu sous les auspices conjointes de la Division des affaires scientifiques de l'OTAN, de l'Université de Montréal et de l'Université Bishop, à Lennoxville, Québec, Canada, du 12 au 25 août 1979. Quelque 16 spécialistes de renommée dans ce domaine présenteront des exposés sur les effets des facteurs chimiques et physiques de l'environnement sur la physiologie des poissons. L'impact global de ces facteurs sur la vie des poissons (rythmes, comportement, etc.) sera aussi examiné. Environ 80 personnes de niveau post-doctoral ou pré-doctoral seront invités à participer. Le préférence sera donnée aux ressortissants des pays membres de l'OTAN. Quelques-unes de ces personnes recevront de l'aide financière pour leurs frais de voyage et/ou de séjour.

Les intéressés sont priés de communiquer avec le directeur du cours :

Professor M. A. Ali
Département de Biologie, Université de Montréal
Case Postale 6128, Montréal, Qué. H3C 3J7

Fjord Oceanographic Workshop

During the week of June 4–8, 1979 a workshop on the general subject of Fjord Oceanography will be hosted at the Institute of Ocean Sciences, Patricia Bay, Vancouver Island, British Columbia. The workshop will be funded by NATO as an Advanced Research Institute.

The workshop will be a multidisciplinary one, and contributions are invited from any scientists working in the general field of fjord oceanography. In general, we invite any contributions on physical, biological, or chemical subjects relevant to fjord oceanography. Topics suggested for discussion include observations and theories of fjord circulation; hydraulic jumps, controls, and transitions; internal waves and tides; mixing processes and deep-water renewal; dynamics of organic material produced in fjords; community exchanges with the open sea; sediment–organism relationships; eutrophication and oxygen budgets. Each session will include a keynote address by a leader in the field followed by the contributed papers.

Limited funds are available to *assist* with travel to and from Victoria. Applications for financial support including an estimate of the applicant's travel costs and an estimate of the amount that might be obtained from other sources should be submitted, with abstracts of proposed contributions, by January 26.

Scientists wishing to attend the workshop should write and notify the Organising Committee, Fjord Oceanography Workshop, Institute of Ocean Sciences Patricia Bay, P.O. Box 6000, 9860 W. Saanich Road, Sidney, B.C. V8L 4B2, Canada. Abstracts of papers should be submitted by March 2, 1979 to the Organising Committee and by February 23, 1979 to the closest member of the Scientific Committee (list available from the Organising Committee).

Atelier de travail océanographique sur les fjords

Un atelier de travail sur le sujet général de l'océanographie des fjords se tiendra à l'Institut des sciences océaniques, Patricia Bay, île Vancouver, Colombie-Britannique. L'OTAN financera cet atelier à titre d'institut de recherches supérieures.

L'atelier de travail sera multidisciplinaire, et les scientifiques oeuvrant dans le domaine général de l'océanographie des fjords sont invités à y présenter des communications. D'une manière générale on acceptera des contributions en physique, biologie ou chimie se rapportant à l'océanographie des fjords. Parmi les sujets de discussion suggérés, on peut noter : observations et théories sur la circulation dans les fjords; ressauts hydrauliques, contrôles et transitions; ondes internes et marées; processus de brassage et renouvellement des eaux profondes; échanges des communautés avec la haute mer; eutrophisation et bilans d'oxygène. Chaque séance comportera une présentation par une autorité, suivie des contributions.

Des fonds limités sont disponibles pour *aider* à défrayer le voyage aller-retour de Victoria. On devra transmettre avant le 26 janvier les demandes d'aide financière, y compris un estimé des frais de voyage du demandeur et un estimé du montant qui pourrait être obtenu d'autres sources, ainsi que les résumés des contributions proposées.

Les scientifiques qui désirent se rendre à cet atelier de travail voudront bien en aviser par écrit le Comité d'organisation, Atelier de travail sur l'océanographie des fjords, Institut des sciences océaniques, Patricia Bay, C.P. 6000, 9860 W. Saanich Road, Sidney, C.-B. V8L 4B2, Canada. Les résumés des contributions devront être soumis avant le 2 mars 1979 au comité d'organisation et avant le 23 février 1979 au membre le plus rapproché du comité scientifique (on pourra s'en procurer la liste auprès du comité d'organisation).

Reproductive Physiology of Fish

Proceedings of an International Symposium

The 51 papers on reproductive physiology of fish, presented by experts in the field at the symposium held at Paimpont (France) from September 19 to 21, 1977, have now been published in a 350-page issue of *Annales de Biologie animale, Biochemie, Biophysique*. The papers are grouped in six categories: Gonadotropine hypophysaire; Axe hypothalamo-hypophysaire; Gonads, cytological observations, Endocrinology of sexual cycles; Vitellogenesis; Temperature and photoperiod; Problèmes d'aquaculture.

Orders should be addressed to the Laboratory of Physiology, I.N.R.A., 78350 Jouy-en-Josas, FRANCE, with a cheque for 65 FF made out to the order of Monsieur l'Agent Comptable du C.N.R.Z., or an invoice may be requested at the time of ordering.

Physiologie de la reproduction des poissons

Comptes rendus d'un colloque international

Les 51 articles traitant de la physiologie de la reproduction des poissons présentés au colloque de Paimpont (France) du 19 au 21 septembre 1977 sont maintenant publiés dans un numéro de 350 pages des *Annales de Biologie Animale, Biochimie, Biophysique*. Les articles sont groupés en six catégories : Gonadotropine hypophysaire; Axe hypothalamo-hypophysaire; Gonades, observations cytologiques, endocrinologie des cycles sexuels; Vitellogénèse; Température et photopériode; Problèmes d'aquaculture.

On voudra bien adresser sa commande au Laboratoire de Physiologie, I.N.R.A., 78350 Jouy-en-Josas, FRANCE, et l'accompagner d'un chèque au montant de 65 FF à l'ordre de Monsieur l'Agent Comptable du C.N.R.Z., ou d'une demande de facturation.

Journal of the Fisheries Research Board of Canada

Guide for Authors

Content

We welcome manuscripts reporting significant new information in the broad fields of fisheries management and technology, ocean science, and aquatic environments relevant to Canada. Manuscripts must not have been submitted or accepted for primary publication elsewhere. In general, manuscripts reporting fragments of research are unacceptable, as are those of mainly local interest.

Articles: Studies of broad scope that are original contributions to science.

Notes: Differ from articles on the basis of scope or completeness, rather than quality of research. They may report significant new knowledge arising from problems with narrow, readily defined limits, or important findings that warrant immediate publication before broader studies are complete. Notes should occupy no more than 3 printed (9 manuscript) pages.

Reviews: Detailed critical appraisals of broad areas of investigation, particularly those that have developed rapidly in recent years.

Perspectives: Essays of opinion or hypothesis on aquatic science that are of concern to the professional and layman. References are desirable; informal style is welcomed.

Letters and Comments: Opinion on topics recently discussed in the *Journal*; preferred maximum length, 500 words.

Editorial Practices

The *CBE Style Manual* (4th ed. AIBS, Arlington, Va. 22209) is used as the authority in matters of form. The standards for spelling are *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (3rd ed. 1970) Spec. Publ. No. 6, American Fisheries Society. All measurements must be metric and SI units are preferred.

Series titles should be avoided. An *abstract* is required for all manuscripts, and should state concisely, in less than 250 words, what was done, found, and concluded. Up to 10 *key words* should follow the abstract.

Each manuscript is normally submitted to two *referees*. Contributors are encouraged to suggest names of potential referees.

Illustrations should be submitted in triplicate as photographic reproductions. They should not be mounted, stapled, or clipped. Symbols, letters, and numerals must be neat, and at least 1.5 mm high when the illustration is reduced to column width. Drawings should, when possible, be grouped to facilitate comparisons.

Proofs are sent to the author, who is responsible for correcting errors in typesetting. *Alterations to the content must be avoided.*

Fifty *reprints* are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent with the proofs). A charge of $40.00 per page is made for articles published. When submitting a manuscript, an author should state that his institution will accept this charge.

Checklist on Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a data or manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the research?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report? Does the *abstract* give the essentials of the new knowledge? Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data? Are generalizations on the *results* adequate? Are findings distinguished from inferences from them? Is *discussion* limited to interpretation and significance of the findings?

Journal de l'office des recherches sur les pêcheries du Canada

Guide des Auteurs

Sujet

Les manuscrits comportant une information nouvelle et significative dans le vaste domaine de la gestion et de la technologie des pêches, des sciences de la mer et des milieux aquatiques au Canada sont les bienvenus. Ils ne devront pas avoir été soumis ou acceptés pour publications dans d'autres périodiques de fonds. En général, les manuscrits portant sur des fragments de recherche sont inacceptables, car ils n'ont qu'un intérêt local.

Articles: Études d'une portée générale, constituant des contributions inédites à la science.

Notes: Se distinguent des articles par la portée et le degré d'achèvement plutôt que par la qualité des recherches. Elles peuvent signaler une connaissance nouvelle et significative découlant de problèmes étroitement limités et facilement définis, ou d'importantes découvertes qui méritent d'être publiées avant que des études plus vastes ne soient terminées. Les notes ne doivent pas dépasser 3 pages imprimées (9 pages de manuscrit).

Critiques: Appréciations critiques détaillées de vastes champs de recherches, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives: Essais portant sur une opinion ou une hypothèse relative aux sciences aquatiques qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Lettres et commentaires: Opinions sur des sujets récemment exposés dans le *Journal*. Longueur maximale préférable: 500 mots.

Disposition générales

Le *CBE Style Manual* (4e éd. AIBS, Arlington, Va. 22209) sert de guide quant à la forme de la présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenus dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (3e éd. 1970) Publ. spéc. n° 6, American Fisheries Society. Toutes les mesures doivent être conformes au système métrique, de préférence en unités SI.

On devra éviter les *articles en séries*. Un *résumé* doit accompagner chaque texte et doit exposer brièvement, en moins de 250 mots, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé. Le résumé doit être suivi d'un nombre de *mots clés* ne dépassant pas 10.

Chaque texte est soumis d'ordinaire à deux *arbitres*. Nous encourageons les collaborateurs à suggérer les noms d'arbitres possibles.

Les *illustrations* doivent être soumises en triple sous forme de reproductions photographiques. Elles ne doivent pas être montées, brochées ni coupées. Les symboles, lettres ou chiffres doivent se détacher avec précision lorsque l'illustration est réduite à la largeur de la colonne. Les dessins doivent, autant que possible, être groupés pour faciliter l'étude comparative.

L'auteur doit revoir les *épreuves* qu'on lui remet et en corriger les erreurs typographiques. *Il doit éviter de changer le contenu du texte.*

Cinquante *tirés à part* sont fournis gratuitement. Des tirés à part supplémentaires peuvent être achetés au moment de la publication. (Un bon de commande à cet effet accompagne les épreuves.) Les frais sont de $40.00 par page pour la publication d'articles. Quand un auteur soumet un manuscrit, il doit préciser que son institution accepte les frais.

Liste de contrôle pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la recherche?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il représentatif du contenu du rapport? Le *résumé* donne-t-il l'essentiel des connaissances nouvelles? L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème? La section *matériel et méthode* contientelle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données? Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions? La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Journal of the Fisheries Research Board of Canada

Guide for Typists Preparing Copy

Read "Guide for Authors". When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize the first letter of each word. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

Type the title, the author's names and affiliations, related footnotes, the running head, the abstract with its bibliographic citation, and key words on the first page (see Appendix A). Number all pages beginning with the title page, including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Scientific Information and Publications Branch.

A detailed guide with appendices is available from the Scientific Information and Publications Branch.

Abbreviations: Abbreviations used frequently in the *Journal* are listed in Appendix B.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).

Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send three photographic reproductions (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write or type on the illustration itself. Also, type the captions in succession on a separate page.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Type names of journals in full.

Headings: If the levels of importance of your heads and subheads are not apparent from their positions, identify each of them with an appropriate circled number or letter in the left-hand margin of the typed page: 1 or A for the highest level, 2 or B for the second level, 3 or C for the third level. Or include with your manuscript a typed list of heads and subheads, indented as necessary to indicate their relative importance.

Journal de l'office des recherches sur les pêcheries du Canada

Guide pour les secrétaires d'auteurs

Lisez le « Guide des auteurs ». Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21.5 × 28 cm (8.5 × 11 pouces). Si possible, employez un papier avec lignes numérotées en marge. Laissez toujours une marge d'au moins. 2.5 cm.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour la première lettre de chaque mot. Pour les petites majuscules, employez les minuscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs, les renvois qui s'y rapportent, le titre courant, le résumé avec sa référence bibliographique et les mots clés (voir annexe A). Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie ainsi que deux copies lisibles à la Direction de l'information et des publications scientifiques.

Un guide détaillé y compris des annexes est disponible gratis de la Direction de l'information et des publications scientifiques.

Abréviations: Nous donnons à l'annexe B une liste d'abréviations communément utilisées dans le *Journal*.

Tableaux: Consultez une copie du *Journal* pour la composition des tableaux (voir annexe C).
Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*:

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et audessous des entêtes et au-dessous des colonnes, rarement ailleurs. Ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

À l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge « Tableau — près d'ici ».

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir annexe C).

Illustrations: Envoyez avec le manuscrit trois reproductions photographiques (21.5 × 28 cm ou moins) pour chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. De plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée.

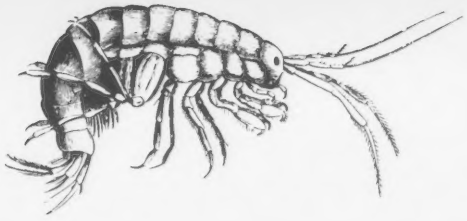
À l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge « Fig. — près d'ici ».

Équations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir annexe D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et la chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le *Journal* (voir annexe E). Ecrivez les noms des périodiques au long.

En-têtes: Si la position de vos en-têtes et sous-en-têtes ne suffit pas à indiquer leurs niveaux d'importance, identifiez chacun d'eux par un chiffre ou une lettre encerclé à la marge gauche de la page dactylographiée: 1 ou A pour le niveau supérieur, 2 ou B pour le deuxième niveau, 3 ou C pour le troisième niveau. Ou encore, transmettez avec votre manuscrit une liste dactylographiée d'en-têtes et de sous-en-têtes rentrés de façon à indiquer leur importance relative.



Aquaculture

Editors - in - Chief: C. E. NASH, *Kramer, Chin and Mayo Inc, Seattle, Wa, U.S.A. -*
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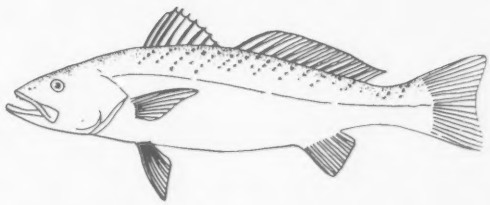
AQUACULTURE is an international journal devoted to research on the exploration, improvement and management of all aquatic food resources, both floristic and faunistic, from freshwater, brackish and marine environments, related directly or indirectly to human consumption. Relevant topics include:



- analysis of environmental requirements of animal and plant species
- exploration of new food resources
- improvement of breed
- fertilization and preparation of fertilizers
- cultivation
- harvesting
- diseases affecting aquatic animal and plant species and their control
- related aspects concerning the conditioning of aquatic habitats, i.e. temperature regulation, engineering, construction and maintenance of rearing equipment.

The effects of water pollution and its control on food resources are also within the scope of the journal.

Subscription Information
1979: Volumes 16 - 18 (12 issues) - US $194.75/Dfl. 399.00 including postage.

For further information or a free sample copy, please contact the publisher.

ELSEVIER

P. O. Box 211, 1000 AE Amsterdam, The Netherlands
52 Vanderbilt Ave., New York, N. Y. 10017

The Dutch guilder price is definitive. US $ prices are subject to exchange rate fluctuations.

Journal of the Fisheries Research Board of Canada

Journal de l'Office des recherches sur les pêcheries du Canada

JFRBAK36(1)1–112(1979)
ISSN 0015-296X

Volume 36, No. 1, January 1979

Volume 36, nº 1, janvier 1979

Phytoplankton ecology of Vancouver Harbor **J. G. Stockner and D. D. Cliff** 1–10

An automated device (AGARS) for studying avoidance of pollutant gradients by aquatic organisms **C. R. Cripe** 11–16

Characterization of particulate organic matter transported by some Cascade Mountain streams **R. J. Naiman and J. R. Sedell** 17–31

Paralytic shellfish toxins in the sea scallop, *Placopecten magellanicus*, in the Bay of Fundy **C. P. Hsu, A. Marchand, Y. Shimizu, and G. G. Sims** 32–36

Entrainment of larval fish by the Douglas Point generating station, Lake Huron, in relation to seasonal succession and distribution **J. R. M. Kelso and J. K. Leslie** 37–41

Deepwater exchange processes in the Saguenay Fjord **G. H. Seibert, R. W. Trites, and S. J. Reid** 42–53

Periodicities in Atlantic Coast striped bass (*Morone saxatilis*) commercial fisheries data **W. Van Winkle, B. L. Kirk, and B. W. Rust** 54–62

Modification of the rheotropic behavior of male rainbow trout (*Salmo gairdneri*) by ovarian fluid **M. E. Emanuel and J. J. Dodson** 63–68

Meristic variation of *Lycodapus mandibularis* (Pisces: Zoarcidae) and oceanic upwelling on the west coast of North America **A. E. Peden** 69–76

Notes

Influences of dieldrin on the growth and body composition of fingerling rainbow trout (*Salmo gairdneri*) fed Oregon Moist Pellets or tubificid worms (*Tubifex* sp.) **G. R. Phillips and D. R. Buhler** 77–80

Comparison of a high volume pump and conventional plankton nets for collecting fish larvae entrained in power plant cooling systems **R. M. Leithiser, K. F. Ehrlich, and A. B. Thum** 81–84

Sublethal effects of environmental acidification on rainbow trout (*Salmo gairdneri*) **C. M. Neville** 84–87

Myxosoma cerebralis: a method for staining spores and other stages with silver nitrate **K. Wolf and M. E. Markiw** 88–89

Precocious sexual development in hatchery-reared and laboratory-maintained male steelhead trout (*Salmo gairdneri*) **S. P. Schmidt and E. W. House** 90–93

Survival and growth of juvenile American lobsters (*Homarus americanus*) after eyestalk ablation **D. J. Trider, E. G. Mason, and J. D. Castell** 93–97

Perspectives

Maybe you can't get there from here: a foreshortened history of research in relation to management of Pacific salmon **P. A. Larkin** 98–106

Book Reviews/Comptes rendus: Marine pollutant transfer (H. L. Windom and R. A. Duce [ed.]) **M. A. Giles**; Disease diagnosis and control in North American Marine Aquaculture. Developments in aquaculture and fisheries science, 6. (C. J. Sindermann [ed.]); **J. E. Stewart**; Introductory dynamic oceanography (S. Pond and G. L. Pickard) **R. Allyn Clarke** 107–109

Coming next month/À paraître le mois prochain 110

Announcements/Avis 111–112

Guides for authors and typists/Guide des auteurs et Guide pour les secrétaires d'auteurs *i–iv*

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